The Behaviour of Mixed-Species Tamarin Groups (*Saguinus labiatus* & *Saguinus fuscicollis*).

by

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Abstract

Saguinus labiatus labiatus and *S. fuscicollis weddelli* form stable mixed-species groups in the wild. This thesis investigates the costs and benefits of such an association, with particular emphasis on determining species differences, the "behavioural differences hypothesis". A nine month field study was conducted in northern Bolivia, which showed that the species differed in mean height used in the forest, method of locomotion, and preferred insect foraging strategies.

Subsequent investigations were conducted on captive single species and mixed-species groups at Belfast Zoo. Preliminary observations of mixed-species groups in standard enclosures and while free-ranging, demonstrated that they behaved in a similar way to their wild counterparts, where the *S. labiatus* had priority of access to food and utilised a higher mean height in the cage. Therefore, it is reasonable to relate the results of captive investigations to the wild situation.

The "behavioural differences hypothesis" was investigated through the presentation of novel objects in various parts of the environment. Both species' reactions to objects varied according to predictions based on their vertical partitioning. *S. labiatus* were found to use a more visually orientated approach than *S. fuscicollis*, and this can be related to insect foraging strategies in the wild.

An experiment was conducted with novel food and non-food objects, in order to test the "social facilitation hypothesis", which predicts that the behaviour of one species can orientate the other towards the presence of food. Results suggest that *S. labiatus* have priority of access to objects and are first to consume food, but *S.fuscicollis* are able to use this behaviour and always gained some food. The results suggest that overall both species benefit from increased foraging efficiency.

The hypothesis that individuals in mixed-species groups benefit from decreased predation through increased vigilance was investigated, and supported, as members of both species were shown to benefit from a decrease in individual vigilance effort, but an overall increase in total vigilance per unit time. This was shown in both general vigilance and in the active monitoring of a threatening stimuli.

Findings are discussed in terms of costs and benefits towards the participants in mixed-species groups, and are compared to the main theoretical viewpoints in the literature.

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Chapter 1 : Mixed-Species Associations : An Introduction.

1.0 General introduction.

Associations occur where two or more species show an aggregation in a non-random manner (e.g Norconk,1990a). Implicit in the definition of association, is that individuals have the opportunity to respond directly to the actions and behaviour of others (e.g. Waser, 1987). These associations exist between organisms that are sympatric, and are found to occur in a diverse range of animals, such as insects (e.g. Hodge & Uetz, 1992), fish (e.g. Allan,1986; Debrot & Myrberg, 1988; Wolf, 1985), bats (e.g. Bradbury 1975), cetaceans (e.g. Pilleri & Knuckley, 1969), birds (e.g. Eguchi *et al.,* 1993; Graves & Gotelli,1993; Mahon *et al.,* 1992; Powell, 1989), ungulates (e.g. Fitzgibbon,1990; Gosling,1980; Sinclair,1985) and primates (e.g. Gautier-Hion & Tutin, 1988; Klein & Klein, 1973; McGraw, 1994; Peres,1991, 1993 a,b; Struhsaker, 1981). Associations vary across a number of variables, most notably timescale, where these events range from a temporary coincidence at a shared feeding resource up to a permanent and stable grouping. While many bird species have been found to fall mainly towards the lower end of this continuum (e.g. Chilton & Sealy, 1987; Diamond, 1981; Klein, 1988), the long lasting associations of primate species are thought to be amongst the most permanent of all known interspecific groupings (e.g. Gartlan & Struhsaker, 1972; Pook & Pook,1982; Ramirez,1984).

Amongst primates, associations are most commonly found in African guenons (*Cercopithecus* : Waser,1987) and in the small South American tamarins (*Saguinus* : Terborgh, 1983). Associations in guenons are not usually as permanent as those found in tamarins and they vary depending upon local ecological factors such as food availability and predation threat (e.g. Cords,1990 a, b). The stability and long term association of tamarins set them apart from the other primate associations, and associations may be very long lasting indeed. For example, Terborgh (1983) describes an association between a study group of emperor and saddle-back tamarins which lasted for at least the three years of his field study. This demonstrates the permanency of association. Within the association, the groups show a high degree of spatial coordination, and can be found close together (typically within 20-50 m of each other) for much of the day. Tamarins have been demonstrated to spend somewhere in the region of 80-100% of their daily activity period together (e.g. Buchanan-Smith,1990a; Peres,1991;

Terborgh, 1983). *Saguinus* species are therefore not only found in long lasting associations, but are usually in close contact with each other.

Plate 1 : *Saguinus labiatus labiatus.*

Plate 2 : *S. fuscicollis weddelli.*

The mixed groups formed between two tamarin species, *Saguinus fuscicollis weddelli* and *S. labiatus labiatus* form the focus of the present study (Plates 1 & 2). Field observations of these primates in northern Bolivia are discussed in the next chapter, and the subsequent four chapters deal with the formation of captive mixed-species groups and the empirical testing of their behaviour in single and mixed-species groups, in order to elucidate the costs and benefits involved in association. In the final chapter, all the data from the field and captivity are brought together and the costs and benefits of association are discussed.

1.1 Why form a group ? : theories for group living.

Hypotheses concerning the function of polyspecific associations are fundamentally the same as the reasons proposed for sociality itself (e.g. Alexander, 1974; Bertram, 1978; van Schaik, 1983; van Schaik & van Hoof,1983; Wrangham, 1980,1983), except that they cannot involve any advantages that are solely due to genetic relatedness (Hamilton,1964), but can involve the parasitism of these events, such as kin directed alarm calls (Sherman,1981).

These selective forces fall into two main categories, improved feeding efficiency, and improved predator detection (Barnard & Thompson, 1985; Bertram, 1978; Krebs & Davies, 1981; Morse,1977,1980; Pulliam, 1973). The specific advantages gained by individuals living in groups are;

1) ***Improved feeding efficiency*** : As a member of a group, an individual can utilise resources more effectively than it could on its own (Caraco,1981; Ekman & Hake, 1988, Krebs, 1974; Pulliam & Millikan,1982).

Benefits of are thought to be gained through the following methods ;

a) <u>Social learning</u> : an individual in a group may benefit from observing the behaviour of others (e.g. Krebs *et al.,* 1972; Krebs, 1973).

b) <u>Beating effect</u> : an individual gains food items (usually insects) displaced by the presence of others (e.g. Diamond,1981; Heatwole, 1965; Rasa,1983).

c) <u>Guides</u> : individuals are directed to the position of food resources (usually fixed in position) by others (e.g. Barnard & Stephens,1983; Ward & Zahavi, 1973).

d) <u>Maximise renewal time and avoid previously used areas</u> : by foraging in a group, individuals systematically use resources and avoid areas that have been already utilised (e.g. Cody,1971).

2) *Improved predator avoidance* : An individual being a member of a group could benefit from better monitoring , detection or disruption of a potential predator than the individual could on its own (Bertram, 1978; Fitzgibbon, 1994; Hamilton,1971; Kruuk,1964; Kenward, 1978; Pulliam & Caraco,1984; Sullivan 1984).

Avoiding predators may be achieved through the following ways ;

a) More eyes and ears : group membership allows more visual and auditory detection of predation threat. This is a statistical increase in the amount of total potential vigilance that is a direct function of group size - more eyes and ears available to detect threats (e.g. Elder & Elder, 1970; Goss-Custard,1970; Morse, 1970,1978; Rasa,1983).

b) Dilution : less chance for each individual of being the prey, classically known as 'safety in numbers'. It is the purely statistical lessening of the chance of being preyed upon, which increases with increasing group size (e.g. Bertram,1978; Fitzgibbon, 1990; Hamilton, 1971).

c) Confusion : the greater number of individuals in a group and its resultant movement, makes it harder for a predator to target its prey (e.g. Charnov *et al.*, 1976; Milinski, 1977,1984; Neill & Cullen,1974; Pitcher,1986).

d) Mobbing : a larger number of individuals may be able to deter a predator through sheer weight of numbers (e.g. Curio,1976; Hoogland & Sherman,1976).

e) Selfish herd : position in group can effect chances of being preyed upon : deviation from 'safety in numbers' due to position in group, usually dominant individuals are in 'safer' positions. (e.g. Hamilton, 1971).

The above mechanisms allow an individual being part of a group to enjoy benefits that are greater than those achieved by the individual being solitary. It is clear that most species live in some sort of grouping, and they presumably benefit from this situation (Pulliam & Caraco, 1984). However, by living in groups the participants involve themselves in a series of costs (Alexander,1974; Bertram, 1978; Godin, 1986; Krebs & Davies,1987; Wilson, 1975). These costs are thought to involve an increase in food competition, more competition for mates and a greater chance of being spotted by a potential predator (e.g. Chapman *et al.*, 1995; Lea, 1984; Milinski, 1979; Pulliam & Caraco,1984; Terborgh & Janson,1986; Vine,1973).

More specifically, it has been hypothesised that limits to the size of a group are imposed by the ecological conditions within which they live. These factors include, the relative amount of food available (e.g.Clark & Mangel,1986; Clutton-Brock & Harvey, 1977; Elgar, 1989; Wrangham,1980,1983), the social system they adopt (e.g. Pulliam & Caraco,1984; van Schaik & van Hoof, 1983) and the level of predation they encounter (e.g. Alexander,1974; van Schaik & van Hoof, 1983). Debate predominantly surrounds the relative strength of the selective pressures exerted by predation and inter-group feeding competition. For example, some authors have suggested that predation is the largest single force acting to promote sociality, and group formation occurs principally to counteract predation through the mechanisms outlined above (Dunbar,1988; van Schaik & van Hoof, 1983; Rowell, 1979; Stacey, 1986). Other authors have argued that inter-group feeding competition may bring about sociality, as large groups may be better at gaining and/or protecting resources (Clutton -Brock & Harvey,1977; Wrangham, 1980, 1983,1987; Wrangham *et al.,* 1993). Individual studies have given support for both theories.

For example, de Ruiter (1986) in a study of scanning and foraging in different sized groups of Capuchin monkeys (*Cebus olivaceus*), found support for the predator defence model, as larger groups had a lower per capita scanning rate but a higher foraging cost. This suggests that individuals being part of larger groups are not as efficient foragers as individuals in smaller groups, but while in the larger groups, the scanning rate of individuals was lower. Other evidence suggests that feeding competition increases with increasing group size in primates (e.g. van Schaik *et al.,* 1983; Waser,1977) and birds (e.g. Barnard & Thompson, 1985; Goss-Custard,1976), and that potential limits on group size are imposed when feeding advantages reach asymptote (Pulliam & Caraco,1984), which may be reached at relatively small group sizes (e.g. Caraco & Wolf,1975). All this suggests that feeding advantages are not the main driving force promoting sociality, because in the cases above, group size was often larger than the size which produced optimal use of resources.

On the other hand, Klein & Klein (1977) report that spider monkeys (*Ateles belzebuth*) split into smaller sub-groups when resources were rare, but were found in larger groups when resources were abundant. Presuming that predation pressure is fairly constant, then the group size appears to vary according to the level of feeding competition. However, the relative contribution of predation to group size may not be clear, as it has been suggested that in some cases the benefits of early warning also reach asymptote fairly quickly (Pulliam & Caraco, 1984) and that groups may be more conspicuous (e.g. Vine,1973).

Whatever the relative outcome of this debate, there is a growing consensus that animals in groups are affected by both predation and feeding competition (van Schaik,1983; Pulliam & Caraco,1984).

1.2 Why form mixed-species groups ?

Increased group size means an increase in resource competition (Altmann, 1974; Dunbar, 1988; Janson & van Schaik,1988; van Schaik,1983; Wrangham, 1980,1987), which is especially true if a group is composed of a single species, and because anti-predator efficiency and foraging efficiency are incompatible when food demand is high (Caraco *et al.*, 1980; Ekman, 1987; Pulliam, 1973). The regulation of single species group size is probably constrained by feeding competition, which may, in areas of high intraspecific food competition, mean that groups are selected to be smaller than the optimal level for predator avoidance (see Pulliam & Caraco,1984).

In areas where predation pressures are great and/or feeding competition is high, then these conflicting pressures can be partially alleviated by the formation of mixed-species groups (e.g. Morse,1977; Peres,1991). Mixed-species groups have been suggested to benefit their participants by giving a reduction in the level of feeding competition that a similarly sized monospecific group would give (e.g. Allan,1986; Berner & Grubb,1985; Caldwell,1981; Peres,1991; Sasvari,1992). Associating with hetero-specifics may also make groups large enough for individuals to facilitate, or perhaps even improve, overall predator avoidance (e.g. Cords,1990a,b; Diamond,1981; Metcalfe,1984; Moynihan,1962; Peres,1991; Thompson & Barnard, 1983).

Individuals in mixed-species groups therefore, can gain the advantages that sociality provides, with reduced intraspecific competition and some added benefits from behavioural differences between the participants. This allows the individual members of the species associating to gain some benefit from the association, due to their differences, but generally there must be some resource overlap between the species, so they can co-exist in the same ecological area (Terborgh,1990).

1.3 Primate mixed-species groups.

Mixed-species groups may be defined as the association between species which are shown to have a non-random coincidence in time and space, whereby members of the different species are found near to each other for a period of time that is not likely to be due to chance alone (see Waser, 1980,1984). The actual criterion set to define such associations may be different for different researchers (e.g. within 20m, Heymann,1990b; within 50m, Buchanan-Smith, 1989). However, other studies of primate mixed-species groups have used an index to define association, which compares the average within species distance with the between species distances (e.g Oates & Whitesides, 1990; Peres, 1991; Whitesides, 1989). This means that a comparison between the intraspecific and interspecific distances may be one method used to determine if an association is taking place. However, in all cases, in order to call a mixed-species group an association, it is necessary to show that the species have a coincidence in time and space (see Waser, 1987).

Relatively few primate species are found to exist in mixed-species associations for any longer than mere "chance" levels (Waser,1987). Where associations occur, they are usually found in the forests of the paleotropics (Bourliere *et al.*, 1970; Gautier-Hion & Gautier, 1974; Struhsaker, 1981) and neotropics (Castro & Soini, 1978; Klein & Klein, 1973; Terborgh, 1983). These areas tend to be species-rich and primates are usually subjected to predation by raptors (Cheney & Wrangham,1987; Terborgh,1990). Species associating tend to be small to medium sized diurnal frugivores or omnivores, that are often ecologically, behaviourally and physically similar (Cords, 1987; Gartlan & Struhsaker, 1972; Peres, 1991). On the other hand, associations are not found in nocturnal prosimians (Charles-Dominique,1977) and orangutans (Rodman,1973), and they are extremely rare in Asian primates (Bernstein,1967; Eudey,1980; MacKinnon & MacKinnon,1980; Southwick & Southwick, 1983).

Long-term stability, where associations occur for a longer duration than chance encounters at a common resource (see Waser,1982,1984,1987), tend to be found only in species of the same genera (e.g. Tamarins :*Saguinus fuscicollis & S. imperator* : Terborgh, 1983 ; Guenons : *Cercopithecus nicititans, C. pogonias & C. cephus* : Gautier-Hion *et al.*, 1983). Interspecific groups of guenons are the most intensively studied associations in the African tropics (Cords,1987,1990a; Gartlan & Struhsaker,1972; Gautier,1988; Gautier-Hion & Tutin, 1988; Hayashi,1975; Marler, 1978; Whitesides,1989). The temporal durations of association are very variable in rate, from infrequent and short aggregations at common resources (Oates &Whitesides,1990; Whitesides,1989), through semi-permanent seasonal groupings (Cords, 1987; Mitani,1991; Struhsaker,1981) up to nearly constant association (Gautier-Hion *et al.*, 1983). These associations may also vary according to local ecological conditions, and not all populations of the same species are found in similar associations (Podolsky,1990; Whitesides, 1989). For example, Cords (1990a) compared the association between *Cercopithecus ascanius & C. mitis* at two sites in East Africa, Kibale in Uganda and Kakamega in Kenya. She found that the species in Kibale only associated for around one quarter of the time those in Kakamega did, and she related this finding to differences in dietary overlap, ecology and the primate communities present at both sites.

Mixed groups comprised of primates from different genera are very rare, presumably due to lower overlap in diet and / or potential predators (Peres,1991). Mixed-species groups of brown capuchins (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*) are a notable exception (Podolsky,1990; Terborgh,1983). Association between these species is temporary, however, lasting from a few hours up to around ten days. Mixed-group formation is probably favoured by their reasonably high dietary overlap and some shared predators (Podolsky,1990; Terborgh,1983). The importance of local conditions for this association are emphasised by a lack of association between the two *Saimiri / Cebus* sub-species found in Costa Rica (*S. oestedii* & *C.capucinus* : Boinski,1989). Another interesting case involves the association between *Procolobus verus* and *Cercopithecus diana*, which despite having a low dietary overlap, were shown to associate due to anti-predator benefits (Oates & Whitesides,1990).

Most of the primate associations described above, last for a fairly short duration and are often dependent upon local ecological factors. The association between members of the South American tamarins, genus *Saguinus* are some of the most permanent, cohesive and long lasting associations of any mixed-species aggregation. The association between two tamarin species, *Saguinus fuscicollis weddelli* and *S. labiatus labiatus* is examined in the present study.

1.4 Behaviour and ecology of tamarins.

1.4.1 Systematics & distribution.

Tamarins and the closely related marmosets, form the *Callitrichidae*, a family of some 25 species of small, arboreal South American primates (Hershkovitz, 1977; Mittermeier *et al.*, 1988; Rylands *et al.*, 1993). The taxonomy used in this thesis is largely based on the seminal work of Hershkovitz (1977), but follows the recent recommended revisions of Rylands *et al.* (1993), taking into account subsequently available new data. Tamarins (genus *Saguinus*) are found in 33 different forms, making up some 12 species (Rylands *et al.*, 1993; Snowdon & Soini,1988 : see Table 1.A) and are widely distributed through the forests of Central and South America, being found as far north as 9° N [Panama / Costa Rica], through equatorial regions, as far south as 24°N [Brazil / Bolivia] (see Rylands *et al.*, 1993). However, their distribution is not continuous, nor has it been exhaustively investigated, but they appear to be limited by major rivers (Ayres & Clutton-Brock, 1992). The northerly populations are isolated in northern Colombia, and *Saguinus* are absent from the Orinoco basin. They occur north of the Amazon river, upwards until the Guianas and south of the Amazon to the west of Rio Madeira, existing in western Brazil, northern Bolivia, eastern Peru and southern Colombia

(Hershkovitz,1977; Rylands *et al.,* 1993; see Figure 1.A). Marmosets (genus *Callithrix*) are distributed west of the Rio Madeira, and share many characteristics with tamarins, such as production of twin infants (Rylands, 1981,1984) and an omnivorous diet (Hubrecht, 1984), but marmosets have an important difference in their dentition, which is specialised for gouging holes in trees to allow exudates to flow (e.g. Stevenson & Rylands, 1988).

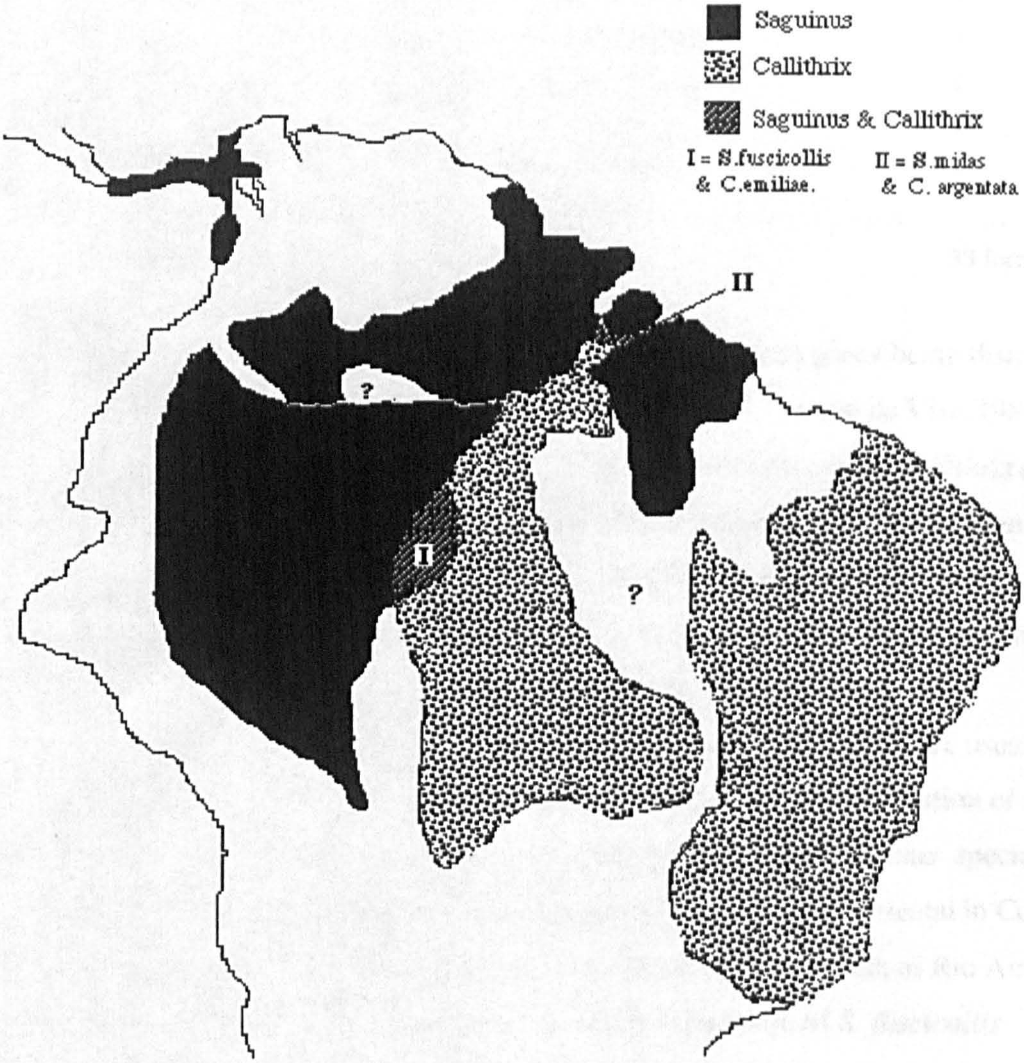

Figure 1.A : Relative distribution of Saguinus and Callithrix species. The main point of separation is the Rio Amazonas, Rio Madeira and Rio Mamore line.

Table 1.A. : Known species of *Saguinus* (After Rylands *et al.*, 1993; Mittermeier *et al.*, 1988; and Thorington, 1988).

Scientific Name	Common Name	No. of Sub-Species
Saguinus nigricollis	Black Mantled tamarin	3
Saguinus fuscicollis	Saddle-back tamarin	13
Saguinus tripartius	Golden mantle tamarin	1
Saguinus mystax	Moustached tamarin	3
Saguinus imperator	Emperor tamarin	2
Saguinus labiatus	Red-bellied tamarin	2
Saguinus inustus	Mottle-faced tamarin	1
Saguinus midas	Golden handed tamarin	2
Saguinus bicolor	Pied, bare faced tamarin	3
Saguinus leucopus	White-footed tamarin	1
Saguinus oedipus	Cotton-top tamarin	1
Saguinus geoffroyi	Geoffroy's tamarin	1
12 Species		33 forms

Marmosets are however, mostly allopatric to tamarins, with each genus being distributed on different sides of the Rio Madeira border (Hershkovitz, 1977; but see de Vivo,1985; Martins *et al.*, 1987 and Ferrari & Lopes Ferrari, 1992 for reports of sympatric *Callithrix emiliae* and *Saguinus fuscicollis*). This means little opportunity exists for association between them.

As the present study concerned tamarins, the policy was to initially concentrate only on comparing the data with studies of tamarin behaviour, unless none existed ; thereby studies on marmoset behaviour were used for comparative purposes.

Individual tamarin species have an interesting distribution, as they are usually found to be sympatric for much of their range, and this is centred around the distribution of the saddle-backed tamarin. The 13 sub-species of this most diminutive of the *Saguinus* species, have the widest distribution of any tamarin, being found east of the Cordillera Oriental in Colombia, Ecuador, Peru and Bolivia and western Brazil, and both north and south of Rio Amazonias (Ferrari & Lopes Ferrari, 1992; Rylands *et al.*, 1993). The range of *S. fuscicollis* is found to encapsulate entirely the distribution of the three members of the *Saguinus mystax* group - *S. labiatus, S.imperator* & *S. mystax* (Hershkovitz,1977), which contains species that are wholly or mostly allopatric to each other (Norconk, 1990b). They are represented by mixed-species groups at all sites where they co-occur (e.g. Buchanan-Smith, 1990a,1991a; Peres,1991; Pook & Pook,1982; Terborgh, 1983). The forces promoting the formation of mixed-species associations, could be as potentially simple as geographic overlap, because the distribution of saddle-backed tamarins is shared, to a lesser or greater extent, by six other callitrichid species, as well as Goeldi's monkey, *Callimico goeldii* (see Table 1.B).

We have the position where the distribution of *S. fuscicollis* overlaps with seven other species and they therefore have the potential to form associations. In reality, the associations found so far, are not as simple as geography might suggest (Table 1.C). While it is clear that polyspecific associations occur with great frequency between *Saguinus fuscicollis* and the *S. mystax* group, (Castro & Soini, 1978; Garber, 1988a; Peres, 1991; Pook & Pook,1982; Terborgh, 1983), the occurrence of other associations may not be greater than random association (Waser, 1982, 1984). These other associations between sympatric species (Table 1.C), appear to be less stable (e.g. *Callimico* & *Saguinus*) and some do not associate at all (e.g. *Cebuella* & *Saguinus*). For example, reports of " observations of apparently mixed groups of *S. nigricollis* with *S. fuscicollis* in the area of Puerto leguizane" (Hernandez-Camacho & Cooper, 1976) is ambiguous as no mention is made of what " mixed species" means in terms of spatial-temporal association, and what exactly the species do when together.

Also, reports of an association between *S. fuscicollis* and *Callimico goeldii* (Buchanan-Smith,1991b; Christen & Geissmann, 1994; Hernandez-Camacho & Cooper, 1976; Pook & Pook, 1982) are not as well documented as other associations, and no researchers have carried out detailed enough observations to show the associations to be anything more than short term. For example, one report states that *Callimico* "associated a great deal with the mixed *Saguinus* troop" (Pook & Pook, 1982 : 196), but they only spent 44% of observation time in "association", and contact time with the study group only amounted to around 37 hours. They also found that the *Callimico* group "did not associate exclusively" with their main study group of tamarins (Pook & Pook, 1982 : 202) , and so the duration, scope and length of association has not yet been clearly defined. However, they do suggest that the pattern was "not the result of coincidental encounters at preferred fruit trees" (Pook & Pook,1981 : 294). Therefore, it is not fully understood whether or not *Callimico* form permanent and long lasting associations with tamarin species.

Table 1.B: Geographical overlap in callitrichids.

Mixed-species associations ---- potential for association.

SPECIES	S.f.	S.n.	S.m.	S.im.	S.la.	S.in.	S.b	S.mi	S.l	S.o	Cal.	Ceb.	Call	Le.
S. fuscicollis	-	√	√	√	√						√	√	√	
S.nigricollis	-	-	?									√	√	
S. mystax	-	-	-									√	√	
S.imperator	-	-	-	-								√	√	
S. labiatus	-	-	-	-	-							?	√	
S. inustus	-	-	-	-	-	-								
S. bicolor	-	-	-	-	-	-	-	√						
S. midas	-	-	-	-	-	-	-	-						
S. leucopus	-	-	-	-	-	-	-	-	-					
S. oedipus	-	-	-	-	-	-	-	-	-	-				
Callithrix	-	-	-	-	-	-	-	-	-	-	-			√
Cebuella	-	-	-	-	-	-	-	-	-	-	-	-	√	
Callimico	-	-	-	-	-	-	-	-	-	-	-	-	-	
Leontopithecus	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Key

√ = overlap is possible. ? = overlap may be possible.

S.f. = *S. fuscicollis* , **S.n.** = *S. nigricollis*, **S.m.** = *S. mystax*, **S.im.** = *S. imperator*, **S. la.** = *S. labiatus*, **S.in.** = *S. inustus*, **S.b.** = *S.bicolor*, **S.mi.** = *S. midas*, **S.l.** = *S. leucopus*, **S.o.** = *S. oedipus*, **Cal.** = *Callithrix*, **Ceb.** = *Cebuella*, **Call.** = *Callimico*, **Le.** = *Leontopithecus*.

In Bolivia, all three members of the *S. mystax* group occur, but they are mostly or wholly allopatric.

Table 1.C : Actual documented associations, so far found.

Mixed-species associations ---- actual associations found.

<u>SPECIES</u>	S.f.	S.n.	S.m.	S.im.	S.la.	S.in.	S.b	S.mi	S.l	S.o	Cal.	Ceb.	Call	Le.
S. fuscicollis		[A]	[B-F]	[G,H]	[I-K]						[N]	[ ]	[I,A]	
S.nigricollis			[?]									[ ]	[?]	
S. mystax												[ ]	[M]	
S.imperator												[ ]	[ ]	
S. labiatus												[ ]	[I]	
S. inustus														
S. bicolor								[ ]						
S. midas														
S. leucopus														
S. oedipus														
Callithrix														[O]
Cebuella													[ ]	
Callimico														
Leontopithecus														

[ ] = Potential Associations

<u>**References**</u>

A : Hernandez-Camacho & Cooper, (1976).
B : Castro & Soini, (1978).
C : Glander *et al.*, (1984).
D : Ramirez, (1984).
E : Garber, (1986,1988a,b).
F : Heymann, (1990b).
G : Freese *et al.*, (1978).
H : Terborgh, (1983)
I : Pook & Pook, (1981,1982).
J : Yoneda, (1981,1984b).
K : Buchanan-Smith, (1989,1990a).
L : Norconk, (1990b).
M : Whitemore (unpubl. data), cited by Pook & Pook, (1982).
N : Ferrari & Lopes-Ferrari, (1992).
O : Rylands, (1989).

The diminutive marmoset *Cebuella pygmaea* clearly does not form any mixed-species groups, despite being sympatric with other callitrichids, and this may be due to their vastly different size, home range size and diet (see Izawa, 1975 ; Ferrari & Lopes-Ferrari, 1989; Soini, 1993, for details on *C. pygmaea*). Martins *et al.* (1987) & Ferrari & Lopes-Ferrari (1992) both reported an association between *S. fuscicollis* and *Callithrix emiliae*, in Rondonia, Brazil. However, on the question of polyspecific association between *Callithrix* and *Saguinus*, Martins *et al.* (1987) state that out of 20 troops studied, only 40% "showed the two species feeding and moving together" and so yet again, the actual details of association are not clear.

Therefore the only consistent and lengthy (both in terms of time per day, and days per year) mixed-species troops are formed between *S. fuscicollis* and members of the *S. mystax* group.

1.4.2 The general ecology of Saguinus.

As there have been relatively few field studies of tamarins, and the types of data collected have been varied, the results of these studies are presented as a general review of the ecology of tamarins. This does not imply that within genus differences and patterns do not occur (see Garber,1993b for a comparison of feeding ecology), but gives a general overview of the behaviour and ecology of tamarins as presently understood.

Tamarins, of the genus *Saguinus*, are small bodied (300-550 g : Hershkovitz, 1977), diurnal and arboreal primates, that usually form groups of 3-13 individuals and utilise territories of between 15 and 100+ hectares, which they defend from conspecifics (e.g. Buchanan-Smith,1990a,1991a,c; Garber,1988a; Kinzey, 1986; Peres,1991; Snowdon & Soini, 1988; Terborgh,1983). Their diet has a variety of foods, including insects, small vertebrates, ripe fruit, plant exudates, gums and nectar (for reviews see Garber,1993b ; Kinzey,1986; Snowdon & Soini,1988). Availability of each component of their diet may be seasonal, with tamarins being fundamentally frugivore-faunivores (Peres,1993a; Terborgh, 1983), but may switch to using nectar (e.g.Terborgh & Stern, 1987; Peres, 1994) or gums (e.g. Garber, 1993a,b) at times of low fruit abundance. The tamarins switch towards these other food sources during the driest months of the year, where they rely on "keystone" resources (Terborgh, 1983) such as nectar from the flowers of *Symphonia globulifera* , and gum from pods of *Parkia* spp. (Buchanan-Smith,1990a; Garber,1988b, 1993b; Heymann, 1990b; Peres,1991). These alternative food sources are small in variety, but make up a large percentage of feeding and foraging time during periods of scarcity (e.g. Peres,1993a). Tamarins are highly skilled in their knowledge of position of food trees, and may make use of 'spatial memory' and or 'cognitive maps' to forage efficiently in their natural environment (Dolins,1993; Garber, 1988b, 1989 ; Garber & Hannon, 1993; Garber *et al.,* 1993c).

Animal prey consumed by tamarins, is an essential and critical part of the overall diet, as they have been shown to spend a similar amount of time foraging for insect prey throughout the year (Peres,1992a). They have also been known to capture small lizards, frogs, birds and to consume eggs when they come across them opportunistically (Neyman,1978; Peres,1992a; Pook & Pook,1982; Snowdon & Soini, 1988).

Tamarin species have been found to be highly territorial, aggressively defending home ranges that contain a mixture of habitat types (Goldizen,1987a; Garber, 1988a; Terborgh, 1983). Home ranges have been shown to be as small as 15 (Buchanan-Smith,1990a) or as large as 149 hectares (Peres,1992b). Rylands (in press) has recently argued that tamarins have evolved in forests that contain gap sites (where trees have fallen) and edge habitat, and so they may require this type of resource in their range. Groups typically defend their territory, which may overlap extensively with neighbouring groups, in aggressive group-group encounters near to the boundaries of their range (Buchanan-Smith,1990a,1991a; Garber, 1988a; Garber *et al.,* 1993a; Peres,1991). These encounters may involve long-call vocalisations, movement towards the periphery of their range, aggressive chases and displacements (e.g. Buchanan-Smith, 1989,1991c). Home ranges are defended only against the same species, even where these species are part of a mixed-species group (Peres,1992b). This aggressive defence does not necessarily mean that the boundaries of territories are 'unsettled' or available, rather it may be that the territories themselves are fixed areas that the groups defend and move between (Terborgh,1983).

Groups of tamarins are typically based around a single breeding female, and in the past they were thought to be exclusively or mostly monogamous (e.g. Neyman,1978). More recently, however, deviations from this basic position have been described, with cases of polyandry and polygyny being recorded (Goldizen, 1987a,b,1988,1989; Garber *et al.,* 1991,1993b; Ruth, 1991). Despite the current debate over tamarin mating systems (see Price, 1990a for a detailed discussion) the main finding is that each group generally has only a single female breeding at any one time (e.g. Pook & Pook,1982; Yoneda,1981,1984a,b) and other females in groups may be reproductively suppressed by the breeding female (as in some captive groups : French *et al.,* 1984). Group size may range from as few as 2 up to 13 individuals (Snowdon & Soini, 1988), but temporary aggregations may be found with up to, and exceeding, 40 or more individuals (Izawa,1976). While groups are usually based around a single breeding female, there are often more males than females in groups (e.g. Garber *et al.*, 1984, 1993b; Terborgh & Goldizen, 1985). All these data suggest that although groups may contain adults of both sexes, breeding females are able to dominate other females and be the only female to reproduce.

Tamarins are predominantly seasonal breeders, with most births being found at the early rainy season, which is around the time of maximum fruit abundance (Pook & Pook, 1981; Soini,1987; Terborgh,1983). This does not mean that births do not occur at other times, but there is a general pattern of few births in the resource-limited dry season (e.g. Moynihan, 1970; Peres,1991). Tamarins typically give birth to non-identical twin infants, and these are carried through the first 10-12 weeks (Price,1990a; Snowdon & Soini,1988). These infants are a high cost energetically to the breeders, as tamarins produce neonates which are relatively large when compared to their own bodyweight (Leutenegger, 1973). Coupling this intensive carrying, high infant weight and the costs of lactation, means that lone females and perhaps single pairs, may not be able to rear offspring on their own (Goldizen,1987a). In captivity fathers may provide much of the early carrying (Cleveland & Snowdon,1984; Price,1990b; Welker & Schafer-Witt, 1987). In the wild there are no published accounts of pairs successfully rearing infants on their own, and infant care may have to be given by other unrelated breeding males (polyandry) or family members (Goldizen,1987a,1989) for successful reproduction. As a result, tamarins are communal rearers, where much of the infant care is also provided by group members other than the parents, and these "helpers" carry the infant and offer / share food with the infants (Feistner, 1985; Feistner & Price,1990; Goldizen, 1987a, Goldizen & Terborgh, 1985; Heymann,1990b, in press; Price,1990a; Savage *et al.*, 1989). They may also participate in acts such as defence against predators, grooming and playing with infants (Peres,1991). Nevertheless, helpers seem to be essential for survival of infants, as Garber *et al.* (1984) suggest that there is a positive correlation between number of adult males and infant survival in *Saguinus mystax.* These actions are not without cost to the individuals undertaking them, and carrying may put severe energetic restrictions on helpers (Goldizen,1987a; Goldizen *et al.*, 1988; Price,1992; Tardif *et al.*, 1993). Helping may be beneficial for the individual helpers involved, as captive tamarins need rearing experience to successfully rear their own offspring (Epple, 1975; Tardif *et al.*, 1984; Snowdon *et al.*, 1985). Also, if the helpers are related to the offspring, then they can benefit through inclusive fitness (Hamilton,1964).

As outlined previously, predation is regarded as a strong selective force, and as a consequence predators may play a large part in the life of *Saguinus* species, although very few accounts of actual predation events appear in the literature (Cheney & Wrangham, 1987). The best available accounts seem to be those of Terborgh (1983), Heymann (1990c) and Peres (1991), where they all discuss the position that raptors are probably the most prevalent predators upon these small-bodied, predominantly arboreal primates. That is not to say that other types of predation do not happen (see Heymann, 1987; for the account of an anaconda, *Eunextes murinus* , preying upon a moustached tamarin, *Saguinus mystax*), but the position seems to be that the most "common" attacks upon callitrichids are those from the raptors that are found throughout the forests of South America (Cheney & Wrangham, 1987). A list of reported predators (Table 1.D) include raptor species such as Harpy eagles (*Harpia harpyja*), Ornate Hawk-eagles (*Spizaetus ornatus*), and Barred forest falcons (*Micrastur fuficollis*), and terrestrial predators such as tayras (*Eira barbara*) and ocelots (*Felis pardalis*).

These are only a list of actual known predators, and Peres (1991) lists other potential aerial predators such as white hawks (*Leucopternis albicollis*) and great black hawks (*Buteogallus urubitinga*). Tamarins may react with alarm calls to other stimuli that are not necessarily predators, such as humans (Neyman,1980), coatis (Peres,1991), parrots and other birds (Heymann, 1990c). This indicates that the threat of predation to these small primates is high, and probably a strong selective force on their ecology and behaviour.

Prior to entering their chosen sleep site, tamarins often show reduced activity and a reduction in calling, where animals behave in a cryptic manner (Caine, 1987; Dawson,1979; Peres,1991). Sleep sites are usually tree holes, forks of branches or dense vine tangles (Buchanan-Smith,1989; Moynihan,1976; Terborgh, 1983; Yoneda, 1984a). Most groups appear to use several different sleep sites, spread through their home range (Peres,1991).

Table 1.D : Actual and potential predators of tamarins, taken from various sources.

POTENTIAL PREDATORS	ACTUAL KNOWN EVENTS		
A: Aerial Predation Threats[1]			
*Harpy eagle (Harpia harpyja)			
*Guianan Crested Eagle (Morphnus guianensis)			
*Black Hawk Eagle (Spizaetus tyrannus)			
Ornate Hawk-eagle (Spizaetus ornatus)	S. fuscicollis	[a,b]	Terborgh & Janson, pers.comm. to Goldizen,1987.
	S. mystax	[b]	Heymann,1990b.
	S. imperator	[a]	Terborgh,1983.
*Black & White Hawk-eagle (Spizastur melanoleucos)			
*Slate-Colored Hawk (Leucopteruis shistacea)			
Bicolored Hawk (Accipiter bicolor)	S. fuscicollis	[a]	Terborgh,1983.
Barred forest-falcon (Micrastur ruficollis)	S.nigricollis	[d]	Izawa,1978.
Red-throated caracara (Daptrius americanus)	S. mystax	[b]	Ramirez,1989.
B: Terrestrial Predation Threats[2]			
Ocelot (Felis pardalis)	S. fuscicollis	[c]	Heymann,1990b.
Anaconda (Eunectes murinus)	S. mystax	[a]	Heymann,1987.
Tayra (Eira barbara)	S. mystax	[b]	Ramirez,1989.
	S.geoffroyi	[d]	Smith, pers. comm. to Moynihan,1970.
	S.midas	[b]	Jansen, pers. comm. to Galef *et al.*, 1976.
*Jaguar (Panthera onca)			
*Margay (Felis wiedi)			
*Jaguarundi (Herpailurus yagouroundi)			
Humans (Homio sapiens)	S. fuscicollis	[a]	Freese *et al.*, 1978

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1. Taken from Brown & Amadon (1968) and Haverschmidt (1968)
   Unpublished Reports from Terborgh, Janson, Wright, Kiltie, and others.

   * Only known as potential predators of tamarins.
   [a] Predatory act observed.
   [b] Unsuccessful attack observed.
   [c] Remains of prey found in faeces of predators.
   [d] Predator seen with prey item.
2. From Caine & Weldon (1989) and Emmons (1987).

Tamarins have been described as mainly foraging and travelling in the middle to lower canopy areas of the forest (Garber, 1991,1992; Peres, 1991; Pook & Pook, 1982; Snowdon & Soini,1988). This area has many medium and large sized, horizontal and obliquely angled branches, which tamarins locomote upon using quadrupedal progression (Fleagle & Mittermeier, 1980; Garber, 1989,1991; Kinzey, 1986). For example, Garber (1991) reports that quadrupedal walking, running and bounding accounted for 40-50% of travel in three different tamarin species. He also found that leaping was a very important form of locomotion, and lists 3 different types of leaps : 1) Acrobatic leaps ; these are 5 metres or more, and are used to cross large gaps in the canopy or for moving between adjacent tree crowns, 2) Bounding leaps ; are less than 2 metres and occur at the end of quadrupedal progression, or 3) Trunk-to-trunk leaps ; are usually between 1 and 2 metres, between medium-large sized vertical trunks found in the undercanopy.

In most tamarin species, the first two types of leaping dominate, but *S. fuscicollis* uniquely show an unusually large amount of trunk-to-trunk leaping (Garber, 1991; Soini, 1987; Terborgh,1983; Yoneda,1984b). This is not to say that all other tamarins do not use this method, or do not cling to large trunks. In fact, the reverse is true ; all tamarins possess claws on all digits except the hallux (Ford, 1980) and they use them to support themselves when on large inclined substrates (Pook & Pook, 1982; Snowdon & Soini, 1988; Thorington,1988). These clawed digits are an adaptation in tamarins and are considered to be superior to clawless digits when travelling on large vertical substrates (Cartmill,1985).

However, amongst tamarin species only *S. fuscicollis* appears to be predominantly adapted for the under canopy area of the forest (Garber,1991). This adaptation is crucial to the role that *S. fuscicollis* plays in its association with members of the *S. mystax* group, and will be covered in detail below.

1.5 The dynamics of mixed-species *Saguinus* troops.

The position where stable associations are only formed between *S. fuscicollis* and the three member species of the *S. mystax* group, is presumably related to the stratification of ecological niches within the forest. Both species have been shown to diverge in type of prey taken, mode of transport used, and preferred vertical height in forest (Buchanan-Smith, 1990a; Garber, 1988a; Heymann, 1990b; Pook & Pook, 1982; Peres,1991; Yoneda, 1981, 1984b). On the other hand, all members of the *S. mystax* group appear to show great similarity in these behaviours (Table 1.E).

Table 1.E: The *S. mystax* group ; within group similarities and behavioural differences with *S. fuscicollis.*

	References
1) Mode of transport	
S. mystax group use quadrupedal walk / run to move about trees.	[1-7]
S. fuscicollis often use vertical clinging and leaping to move.	[1-7]
2) Height of travel	
S. mystax group travel at a higher mean height than the *S. fuscicollis.*	[1-7]
3) Foraging height	
S. mystax group forage for prey at a higher mean height than the *S. fuscicollis.*	[1-7]
4) Method of foraging	
S. fuscicollis use a probing style of insect foraging in knots in wood, holes etc.	[1-7]
S. mystax group use a "hunt & catch"method, gaining insects from leaves etc.	[1-7]
5) Prey size	
S. mystax group will gain smaller food items from hunting than the larger embedded insects caught by *S. fuscicollis.*	[1, 4-7]

Key to References

S. labiatus & *S. fuscicollis*	1. Yoneda (1981,1984b). 2. Pook & Pook (1982). 3. Buchanan-Smith (1989,1990a)
S. labiatus & *S. mystax*	4. Castro & Soini (1978). 5. Norconk (1990b). 6. Peres (1991).
S. labiatus & *S.imperator*	7. Terborgh (1983).

1.5.1 Vertical stratification between associating tamarins.

An interesting patterning of behaviour occurs with the associating species, where there is a stratification in terms of vertical separation and mode of locomotion used (Castro & Soini, 1978; Peres, 1991; Pook & Pook, 1982; Terborgh, 1983; Yoneda, 1981, 1984b). In the majority of cases described so far, *S. fuscicollis* occupies a lower portion of the forest than the sympatric species and it also locomotes largely by means of vertical clinging and leaping from trunk to trunk (Buchanan-Smith, 1989; Pook & Pook, 1982; Yoneda, 1981; see Table 1.F). Norconk (1990b) has quantified these differences for *S. mystax* and *S. fuscicollis,* where she produced a comprehensive list of activity categories (e.g. Rest, Travel, Vigilance, etc), and found that in all of them *S. mystax* used a higher mean height. This is generally found throughout the *S. mystax* group (see Table 1.E), where they invariably occupy higher portions of the forest than the *S. fuscicollis* and locomote by using quadrupedal walking (e.g. Buchanan-Smith, 1990a; Norconk, 1990b; Peres, 1991).

Table 1.F : Vertical stratification of *Saguinus* species involved in associations.

Activity	Modal Height Range		Reference
	S. fuscicollis	*S. mystax*	
Locomotion	5-8m	9-12m	Norconk,1990b
Insect Foraging	4-6m	9-11m	Peres, 1991
	S. fuscicollis	*S.imperator*	
Fruit feeding*	20-25m	20-25m	Terborgh, 1983
	S. fuscicollis	*S. labiatus*	
Forage +Travel	2-5m	5-10m	Pook & Pook,1982
All	5-10m	10-20m	Yoneda, 1984b
Travel	2-5m	5-10m	Yoneda, 1984b
Forage for prey	0-5m	5-10m	Yoneda, 1981
Feed on fruit*	10-20m	10-20m	Yoneda, 1981
All**	10-15m	10-15m	Cameron *et al*, 1988
All	10-15m	16-20m	Buchanan-Smith,1990a

* There is a suggestion that the two species may predominantly feed on the same fruits, so not surprising if this is at the same height (Terborgh,1983; Buchanan- Smith , 1990a)

** This may be a consequence of the census technique, which only noted the species when encountered (usually startled ?) during a census.

1.5.2 Insect foraging differences.

Yoneda (1981), in a study of *S. labiatus* and *S. fuscicollis*, noticed that although they competed for fruits (ate a similar range of fruits), they showed a divergence in pattern of insect foraging and prey size. *S. labiatus* predominantly took smaller insects from higher up, using a "seize and capture" technique, while *S. fuscicollis* usually foraged lower down, in hollows and gaps, probing for insects. This divergence in strategy of insect foraging, means that the two species are not competing for insects, but are in competition for fruit (in terms of dietary overlap, at least). A similar pattern has been found for all members of the *S. mystax* group (Garber, 1993b; Peres,1991; Pook & Pook, 1982; Terborgh, 1983; Yoneda, 1981,1984b).

1.5.3 Agonism, interaction and cohesion between the species.

In agonistic interaction between the two associating species, it appears that *S. fuscicollis* usually withdraws away from the other *Saguinus* species, especially in feeding trees (Heymann, 1990b; Peres,1991; Terborgh,1983; see Table 1.G). There is a tendency for agonistic encounters to happen in small feeding trees (Heymann, 1990b) and this is where the associating species' high dietary overlap (e.g. Buchanan-Smith, 1989; Peres,1993a; Terborgh, 1983) becomes a source of contention, and competition will be strongest. Agonism usually takes the form of a displacement from the desired area (Heymann, 1990b). Peres (1991) has demonstrated that *S. fuscicollis* are often displaced from small monopolisable undercanopy trees by their congeners, even though they usually discover them.

TABLE 1.G : Priority of access to resources in mixed-species troops of *S. fuscicollis* and members of the *S. mystax* group.

	Pattern of Interactions	N	Reference
S. labiatus	Threats, no fights reported		Yoneda, 1981
	labiatus > fuscicollis	2	Pook & Pook, 1982
	labiatus > fuscicollis	1	Buchanan-Smith, 1989
S. mystax	?	?	Castro & Soini, 1978
	mystax > fuscicollis	108	Heymann, 1990b
	mystax > fuscicollis	4	Norconk, 1990b
	mystax > fuscicollis	62	Peres, 1991
S. imperator	imperator > fuscicollis	?	Terborgh 1983

> = Has priority of access. In effect, this usually means that this species can displace the other species from a desired place (e.g. a feeding tree)

However, this is not a large cost for *S. fuscicollis*, as most of their food sources are comprised of large superabundant non-monopolisable trees (Peres, 1993a). In such trees both species may feed together (i.e. in parallel) or the *S. fuscicollis* may enter as their congeners exit (i.e. feed in series), suggesting little competition between them. In fact, it appears that the congeners may lead the *S. fuscicollis* to these large resources (e.g. Buchanan-Smith,1989; Peres,1991). Overall the cost of feeding competition to both species appears to be minimal.

In territorial encounters, there is a tendency for the absence of interspecific aggression (Buchanan-Smith, 1989; Garber, 1988a; Pook & Pook,1982). Both species are highly territorial towards their conspecifics and expend a great deal of energy and time defending the resources from them (e.g. Garber,1988a). This may often occur in parallel, with both members of a mixed-species group defending their territory from neighbouring groups. These encounters are usually centred around important feeding trees (Garber, 1988a; Peres, 1992a). However, in general, there are few interactions, both agonistic and friendly, between associating species (Buchanan-Smith, 1990a; Heymann, 1990b;Norconk, 1990b; Yoneda, 1981).

The cohesion of a mixed-species troop is usually quite high, with associations occurring in the region of 50-100% of the time (Buchanan-Smith, 1989; Peres, 1992a; Pook & Pook, 1982; see Table 1.H). The associating species form a very cohesive troop, and are usually found between 20m (Heymann,1990b) and 50m of each other (Buchanan-Smith, 1990a). Cohesion of the troop may be facilitated by intergroup long call vocalisations, both in the morning and when the two groups become separated, as both species respond to each others' calls (Buchanan-Smith, 1989,1990a; Castro & Soini, 1978; Heymann, 1990b).

Table 1.H : Degree of association between members of *Saguinus* mixed-species groups (Note that every study has its own definition of "association").

Saguinus fuscicollis & Saguinus mystax.
(Saddle-backed tamarins & Moustached tamarins)

% Association	Study site	Reference
58.3	RIO BLANCHO (NE Peru)	Castro & Soini, 1978
52.9	LOS ANGELES (NE Peru)	Glander *et al.*, 1984
-----	SANTA CECILIA (NE Peru)	Glander *et al.*, 1984
100	RIO YARAPA (NE Peru)	Ramirez, 1984
74.0	RIO BLANCHO (NE Peru)	Garber, 1988a,b
72.0	RIO BLANCHO (NE Peru)	Heymann, 1990b
98.0	RIO URUCU (NW Brazil)	Peres, 1991

Saguinus fuscicollis & Saguinus labiatus
(Saddle-backed tamarins & Red bellied tamarins)

% Association	Study site	Reference
75.9	COBIJA (NW Bolivia)	Pook & Pook, 1982
83.8	COBIJA (NW Bolivia)	Buchanan-Smith, 1989
-----	MUCDEN (N Bolivia)	Yoneda, 1981, 1984b

Saguinus fuscicollis & Saguinus imperator
(Saddle-backed tamarins & Emperor tamarins)

% Association	Study site	Reference
100	COCHA CASHU (SE Peru)	Freese *et al.*, 1978
----	COCHA CASHU (SE Peru)	Terborgh, 1983

Saguinus fuscicollis & Saguinus nigricollis
(Saddle-backed tamarins & Black mantled tamarins)

% Association	Study site	Reference
----	PUERTO LEGUIZAMO (S Colombia)	Hernandez-Camacho & Cooper, 1976

KEY : --- = Not noted specifically.

1.6 Conditions necessary for forming *Saguinus* associations ?.

As discussed previously (Section 1.4.1), the associations found to occur are not as simple as mere geographical overlap. There is also cause to conclude that the *Saguinus* species that associate need to have a great similarity in ecological niche (Section 1.4.2) as well as some divergence (Section 1.5). This may apply to the members of the *S. mystax* group, who utilise a niche that is very similar (although not identical) to that of *S. fuscicollis* . On the other hand, this will probably not be the case in other species of primates which are sympatric, but do not form associations ; they may have more divergent ecologies. The individual members of the *S. mystax* group, appear to occupy niches that are TOO similar to each other, and as a result cannot live sympatrically.

There seems to be a subtle interplay between factors, so that associating species; (a) have an overlap in terms of resources utilised, where these resources are presumably not too scarce or inter-specific competition would prevent associations being advantageous, but on the other hand, the overlap needs to be of sufficient magnitude to allow the participants to benefit from associations, (b) have the potential to exhibit mutually useful behaviour such as alarm calling, and (c) have a sufficient number of differences in other behaviours and resources utilised, so as not too be of too great a competitor to the associating species. Arguably, the specialisation of *S. fuscicollis* to the lower areas of the forest, and the corresponding difference in insect capture technique from the *S. mystax* group, reduces potential competition and allows these associations to be viable.

We therefore have two main necessary, but not sufficient conditions, to explain the association of *S. fuscicollis* with other tamarin species;

i) geographic ; i.e overlap in distribution

ii) stratification ; i.e. division of some subset of resources.

This offers the scenario where species are ABLE to associate because of differences, but need to have sufficient similarities so that it can be viable to associate (i.e. a compromise between needing some different resources that may be utilised without competition from the associating species, as well as some common resources that must be plentiful enough for both species to utilise without severe competition). This could be represented as follows;

Degree of Overlap in Resource Utilisation Between Species

```
---------No Overlap----->---->----->----->----->-----Total Overlap---------
                X                                               +
B < C           X                  B >C                         +    B < C
                X                                               +
-----------------------------------------------------------------------------
```

X = Theoretical "cut off point" below which not enough resources are shared between species, to allow association to be a viable option.

+ = Cut-off Point, above which, the species are competing TOO much for resources (which are not unlimited), so that association is not beneficial.

B = Benefit for a species in associating.

C = Cost for a species when forming an association.

Figure 1.B: Theoretical costs and benefits of association, in terms of resource overlap and interspecific competition.

From Figure 1.B, it is clear that in order to place the species in a particular place, it is first necessary to work out both the costs and benefits involved in the association, and in particular, what "drives" each species to form mixed species troops. It is clear that *S. fuscicollis* and members of the *S. mystax* group have reasons for associating that are greater than merely being ABLE to associate. But what else may be important ? Why are the *S. mystax* group so attractive for *S. fuscicollis* to associate with ? and of course, vice versa ? This has to be framed in the context of a cost-benefit analysis.

This thesis takes the approach of generating specific hypotheses which are testable themselves (or predict behaviour that is itself testable) and produce empirical data that can give a comparison of the relative value of association for both species. The main comparison is an examination between the species, pinpointing which behaviours are both similar and different between them. This allows an evaluation of what may be important to each species, and can help to clarify the costs and benefits of associating. One thing that is important to grasp, is that the costs and benefits affecting each species may not be the same.

Initially this will be examined in terms of an evaluation of the relative merits of the various hypotheses put forward to explain *Saguinus* associations. All known empirical studies will be discussed, and costs and benefits for both species are discussed.

1.7 Evaluation of hypotheses for the formation of tamarin mixed-species troops.

1.7.1 Why associate ?

In the literature, the position of *Saguinus* seems to be dominated by three areas : **Predator avoidance** (e.g. Heymann, 1990b; Norconk, 1990a,b) **Territorial defence** (e.g. Garber, 1988a; Terborgh, 1983) and **Feeding efficiency** (e.g. Peres,1991). It is likely that these three areas provide the main forces driving the species to associate. The level of analysis of these hypotheses has to be that of the various costs and benefits associated with each species performing each behaviour. This enables the quantification and evaluation of the reasons why one group of tamarins would associate with a group from another species of tamarins.

With this idea in mind, association will be examined in the form of specific hypotheses and predictions. This approach has been successfully used by other researchers (e.g. Heymann, 1990b; Peres, 1991).

1.7.2 Feeding efficiency in mixed-species groups of tamarins.

Overall feeding competition between associating tamarins has been shown to be reduced because of a divergence in the type of insect prey consumed. Members of the *S. mystax* group use a visually orientated seize and capture method on resting, mobile prey, where they search leaves and branches in the midstory area (Buchanan-Smith,1990a,1991a; Peres,1991; Pook & Pook,1982). *S. fuscicollis* use a mainly extractive, manipulative strategy, gaining immobile and hidden insects (Garber, 1993a,b; Terborgh,1983; Yoneda,1984a,b). Peres (1991, 1992a) has shown that the species do not overlap greatly in size and class of prey consumed, and that *S. fuscicollis* can gain large orthopterans that are displaced by the higher up *S. mystax*. These species were shown to have few aggressive interactions while insect foraging. Feeding competition for individuals would thus be reduced when compared to competition between members of similarly sized monospecific groups.

Although there is a large overlap in plant food items between the species (e.g. Buchanan-Smith,1990a; Garber, 1988a,1993a,b; Terborgh, 1983), in most circumstances there is little agonism between the species. This is because the majority of plant food resources are large enough for all members of the mixed-species group to feed in (Peres, 1991).

1.7.3 Increased resource defence potential of tamarin mixed-species groups.

Both Garber (1988a) and Peres (1992a) have hypothesised that a mixed-species group will be better at defending their jointly held territory. Garber (1988a) has shown that in mixed-species groups, ability to defend resources was correlated with troop size, where larger troops could defend these resources better, and the cost to smaller groups was increased travel and lowered foraging efficiency. Peres (1992a), also found that mixed-groups spend much effort defending their territory from neighbouring groups, but that *S. fuscicollis* contributed less and gained more from joint defence. This was linked to their reliance on depletable, extracted insects, which were found in higher numbers in the centre of their territory, and the larger impact of intraspecific competition on these resources (Peres,1991,1992a).There appears to be no interspecific territorial encounters mentioned in the literature, so the importance of the associating species in encounters remains unclear. There may be cause to believe that mixed-species gain not in the short-term, but in the long term, with higher reproductive rates due to increased length of tenure (i.e. higher survival, etc. of offspring ; Garber, 1988a; Terborgh, 1983). This remains to be tested.

1.7.4 Avoiding predators by living in tamarin mixed-species groups.

In terms of avoiding predation, there seem to be several mechanisms whereby predation avoidance is achieved through sociality (see Section 1.1). Terborgh (1990: 93) indicates that for these mechanisms, none of them "require that social groups be comprised of a single species" and suggests this may be what drives the mixed-species groups to associate together. This theory sets the scenario where one of the main reasons for the emergence of an association can be tied in with the occurrence of a high rate of predation coupled with the inability of individuals in small groups to deal with it as effectively as they would if they aggregated in larger groups. This is probably the most widely proposed reason for association, but its importance is disputed.

For example, Terborgh (1983) discounted the idea of predation being an important force in the formation of *Saguinus* polyspecific associations, suggesting that ecological factors, such as feeding competition are more valid. He further argues that the way *Saguinus fuscicollis* and *Saguinus imperator* act, are not the optimal strategy to pursue, if predation was the main force shaping association. He lists several facets of behaviour that he feels do not coincide with the predation hypothesis.

1) He argues that if both species help each other to watch for predators, "there would be an approximately equal exchange.......each is sensitive to the other's alarm calls" (Terborgh,1983: 182).

2) Groups that are associated spend much of their time apart, or at least out of visual contact [1] The preponderance of attacks when animals were in tall trees, coupled with the frequently sequential nature of feeding, led Terborgh to conclude that the potential for reciprocal warning of predator approach is reduced.

---

[1] Around 10-20m, is approximately the limit of visual contact (Terborgh,1983: 182)

3) Terborgh also concludes that taking advantage of safety in numbers, and extra eyes and ears, would predict that mutual toleration during feeding would occur.

His clear conclusion was that the "two groups do not behave in such a way as to maximise their ability to reciprocate in predator warnings" (Terborgh, 1983: 183).

On the other hand, these criticisms are fairly vague, and can be questioned. For example, there is no need for an "equal exchange" in alarm calls (point 1), as long as both species alarm call when they detect potential predators. There is evidence to suggest that for both species the costs and benefits do not need to be identical. Peres (1991) has shown that both species provide warning of potential predators, and the the higher up *S. mystax* are more responsible for detecting aerial predators, and scan upwards more frequently than their congeners. The *S. fuscicollis* show more scanning towards terrestrial predators, and as a result spot more potential predators in this area. Peres (1991) argues that the *S. mystax* put more effort into scanning, and suggests that the two species both gain from the other, but these gains are not necessarily identical.

Other criticisms are that, as the alarm calls are vocalisations, then it does not matter if the species are "out of visual contact" (point 2). If one species reacts to the calls of another that is close by, then this will allow an increased probability of avoiding predators, when compared to that of the group on its own. For the idea that "mutual toleration" (point 3), during feeding would be predicted if predator avoidance was the main selective force, negates the possibility that having one species feeding at a time may be a division of labour (i.e. one species eating, the other being vigilant).

Although Terborgh (1983) has discounted the notion of predation being the main selective force promoting mixed-species groups, an evaluation of his arguments suggest that the opposite may be the case. The field study of Peres (1991), provides convincing evidence that the members of a mixed-species tamarin group may benefit from the actions of their congeners. Terborgh (1983) appears to look for an equality of interchange between the species in alarm calling, while Peres (1991) has shown that the two species diverge in the way they scan for predators, each specialising in looking for a different classes of potential predators. The mixed-species group therefore, can gain a level of predator detection that is different and probably superior to, the amount shown by a similarly sized monospecific group of either species.

1.7.5 Overall evaluation of theories.

In his more recent work, however, Terborgh seems to be more aware of creating a balance of predation and competition costs amongst associating groups. Indeed, he makes some comparison between the "closed habitat" associations of Amazonian bird species, and the associations of Amazonian primates (Terborgh, 1990). He has reached a more satisfactory conclusion where "group limiting constraints of feeding competition interact with optimal predator avoidance to strike compromises at variable, but restricted group sizes" (Terborgh, 1990: 94). He suggests that the mixed-species groups of Amazonian primates should be relatively small, of fairly consistent size, and be composed of few to many equally represented species, that may be cryptic, but not convergent in their appearances and that the maximal advantage is derived from alarm signals in alerting one another to the threat of predators. Terborgh (1990 : 95) qualifies this by saying that it would be "limited to troops that share overlapping home ranges", which would give the opportunity of the same heterospecific groups to form and reform repeatedly.

The advantage of mixed-species troops mean that an increase in the number of individuals can occur, without the feeding competition that would occur with a monospecific group. Where food sources are restricted, or specialist knowledge of their location are critical for success (as for *Saguinus fuscicollis*, Terborgh & Stern, 1987), then intraspecific competition for access to these critical resources will be very high, and give a resultant constraint upon intraspecific group size (Terborgh, 1983; van Schaik et al., 1983; van Schaik & van Hoof,1983; Terborgh & Janson,1986).

This means that the anti- predator effect and the intraspecific competition ideas are diametrically opposed at the single species level, but this can be alleviated at least partially, if the groups can associate with another species that does not totally compete for resources.

The high predation rate encountered in Coca Cashu (Terborgh,1983; Cheney & Seyfarth,1987) may be amongst the highest recorded for any non-human primate community. This may also be compounded by the fact that it has a high population density of primates (Terborgh,1983), which will exacerbate the problem of both inter- and intraspecific competition, and may thus account partially for the sequential or parallel feeding described by Terborgh (1983) for *Saguinus.* Indeed, the influence of both factors on the associations may vary with site (van Schaik & van Hoof,1983), and Buchanan-Smith (1990a: 210) reports that "both species (in *S. fuscicollis* & *S. labiatus*, in Bolivia) often fed in the same tree........fed on the same plant material, and their preferred height for eating plant material was also similar".

Peres (1991) found that *S. fuscicollis* and *S. mystax* shared large feeding trees without competition. If this is a more common interpretation of the position in *Saguinus*, then the fact that they tend to feed together in the same fruit trees, will give the predation hypothesis more precedence than Terborgh (1983) originally assigned it. Heymann (1990b) suggests that the mere increase in number of potentially vigilant individuals may be sufficiently advantageous for the formation of mixed-species troops in tamarins, while Peres (1991; 1992a) found a divergence in anti-predator behaviour in mixed-species groups of *S. mystax* and *S. fuscicollis*. He demonstrated a division of labour between the species, as the higher up *S. mystax* spent more time scanning at higher levels of the forest and detected more threats from aerial predators, while the lower down *S. fuscicollis* showed more vigilance at lower areas and detected more terrestrial predation threats. This was also clearly shown by levels of alarm calling which too had the variation linked to height. Finally, Peres (1991 : 195) demonstrated that although some feeding competition occurred between species, most plant resources were "...superabundant, ...most or all individuals of both species fed together in the absence of interference competition."

Breeding competition may be another vital reason for the formation of mixed-species groups (Buchanan-Smith,1989; Peres,1991). This can explain the significance of small intraspecific groups of tamarins; all field studies (e.g. Buchanan-Smith, 1989; Garber,1980a; Terborgh,1983; Moynihan,1976; Neyman, 1980 etc) have found only one breeding female at a time. Monospecific group size is probably also limited by the availability of breeding females, as most groups only have a single, dominant breeding female that reproductively suppresses subordinant females. The position of males are not clear, as there may be polyandrous (i.e. more than one male) matings, but paternity has not been ascribed and both males contribute to rearing the offspring (Goldizen,1989, 1990; Terborgh & Goldizen,1985). There may also be sexually mature male offspring present in their natal groups (Goldizen,1987b; 1988). Thus large groups of tamarins containing adults will have sexually redundant females at least, and probably males as well, making large monospecific groups a reproductive liability for some of its members. This may put restrictions on the size of monospecific groups, as an increased number of different individuals can breed, if a larger number of small groups are formed, rather than a small number of large groups.

In summary, mixed-species groups can be thought to offer similar or enhanced predator detection as equivalently sized monospecific groups. However, the mixed groups probably offer a relatively smaller amount of feeding competition for the participants, and an improved defence of resources. Competition for breeding positions may also place limits on the monospecific group size, and formation of mixed-species groups will give the benefits of large group size, without the costs of intraspecific breeding competition.

1.8 Investigations in the present study.

Despite the three broad areas of theories being presented as separate units, there is some sense in examining the association in terms of one main subject area ; **Social facilitation of behaviour or actions.** This describes the situation where there are distinct facets of behaviour that are species specific, but may additionally give advantage to the other species forming the association. This seems to be something that is almost universally proposed, but there is little empirical evidence to back it up (for a notable exception see Peres,1991,1992a,b). It is also implicated within the framework of all the main hypotheses, and can lead to useful pointers towards what each species gains from associating. Facilitation of behaviour can involve situations such as ;

a) The position of local scarce resources, or
b) Ability to deal with or spot a potential predator, or
c) Newly discovered food sources

For example, the response of a mixed group of *S. fuscicollis* and *S. mystax*, to a snake was strikingly different, with *S. fuscicollis* mobbing the snake, while *S. mystax* remained out of sight, and only rejoined *S. fuscicollis* shortly afterwards (Bartecki & Heymann, 1987). On the other hand, *S. mystax* occupy higher portions of the forest than *S. fuscicollis* and are better at spotting aerial predators (e.g. raptors ; Heymann, 1990b, Peres,1991). This suggests that both species may have knowledge about distinct situations which can be mutually beneficial.

The behavioural differences hypothesis.

This may be phrased as an overall hypothesis to be tested throughout this thesis.

"Each species will have some behavioural patterns distinct from the other species. There may be specific occasions where these behaviours are advantageous, both to the individuals in the species carrying them out and also to the individuals of the other species. The net result can be shared advantage, through social facilitation., i.e. one species may benefit from the behaviour of the other species"

The hypothesis can lead to the prediction that each species may tend to behave differently, or to a different degree, in some specific situation (e.g. exposure to predators, as above), which could bring about a certain reaction that benefits the other species. The range of these behaviours would be different for mixed groups, when compared to monospecific groups. Behaviours may be either shown in an all-or-nothing manner, where one does it and the other doesn't, or they may both show it, but to different degrees. Such benefits may be gained instantly, when the actions of one individual or group of one species can be used immediately by individuals of the other species. An example of this type of facilitation could involve the approach of *S. labiatus* to a feeding tree that has ripe fruit, and this behaviour may guide *S. fuscicollis* to the resource. This is the type of social facilitation which is tested in this thesis. The other type of facilitation relates to behavioural actions that one species witnesses, but does not use it at that particular time. For example, if an individual of *S. fuscicollis* observes predation upon *S. labiatus,* it may react to the presence of this predator in the future due to the action it has observed. This type of social facilitation is beyond the scope of the current study.

The "behavioural differences hypothesis" will be examined over the course of this thesis, for mixed-species *Saguinus labiatus* and *S. fuscicollis* troops, in their natural environment, and in both mixed and monospecific groups in captivity.

1.9 Overall aims and scope of the present study.

(1) The main objective of this thesis is to examine the similarities and differences in behaviour and ecology of *Saguinus labiatus* (red bellied tamarins) and *S. fuscicollis* (saddle-backed tamarins) mixed-species groups, and to relate these to the association between the two species.

(2) A 9-month field study was conducted in the Pando Department of north western Bolivia. The behaviour, ecology and group sizes of groups of both species of tamarin are described. Data are compared and contrasted both between the species and with other studies (Chapter 2).

(3) Captive groups of mixed-species tamarins were formed at Belfast Zoological Gardens, and recommendations and methodology for use in future formation of mixed groups were developed. An experimental study of the behaviour of saddle-backed and red-bellied tamarins was carried out : the methods used in the captive research are outlined (Chapter 3).

(4) A mixed-species troop of 2 saddle-back and 2 red-bellied tamarins were allowed to free-range in a wooded area of approximately 550m^2 for a period of 3 months. Data were collected on activity budgets, spatial relations, ranging and interaction between the

species. In an additional study, the behaviour, interaction and spatial relations in captive tamarin mixed-species groups are now examined (Chapter 4). These measures allowed a detailed examination of the behaviour of both species in captivity, giving an evaluation of how the behaviour of captive tamarins compared with those of wild tamarins.

(5) Tamarins have been shown to investigate and react to objects in their environments. These may be novel non-food or food objects, or they may be stimuli that are threatening to the tamarins (Chapters 5- 6). Learning whether an object is a source of food is very important to tamarins, and the ability of both species to learn the properties of new objects were first tested monospecifically and then in mixed groups (Chapter 5). These tests initially compared the reaction of both species to a set of novel non-food objects and then involved a test of their ability to discriminate between a comprehensive set of both food and non-food objects.

(6) How the two species monitored their environment for potential predators was now examined, as was their reaction to the presentation of threatening stimuli (Chapter 6). This again involved a comparison between the species, both monospecifically and when in mixed-species groups. The anti-predatory role of each species is then discussed, as are possible benefits of being in association.

(7) The differences and similarities between the two associating species are brought together, and changes in behaviour due to association are discussed. This is presented in the broader context of costs and benefits for the participants of associations, and an evaluation of the various theories used to explain association is undertaken.

Chapter 2 : The Behaviour of Wild Mixed *Saguinus labiatus labiatus* and *Saguinus fuscicollis weddelli* Groups in Northern Bolivia.

2.0 Introduction.

Although *Saguinus l. labiatus* is found in eastern Peru and northwestern Brazil (see Chapter 1), it is only in the remote north-westerly Pando region of Bolivia that its behaviour has been studied in detail. Initial reports of the association between *S. labiatus* and *S. fuscicollis* appeared in the early eighties (Yoneda,1981; Pook & Pook,1982), but a lack of subsequent research meant that this association was not studied in as much detail as the other *Saguinus* associations. For example, *S. mystax* and *S. fuscicollis* have been the subject of much intensive work (e.g. Heymann, 1990b; Garber,1988a,b; Norconk,1986,1990b; Peres,1991,1992a,b) and *S. imperator* and *S. fuscicollis* were part of probably the most intensive study of any New World primates, namely that of Terborgh (1983) in Manu National Park, Peru.

However, one more detailed study of *S. labiatus* and *S. fuscicollis* was done between July and December 1987, involving the capture and subsequent radio-tracking of individuals (Buchanan-Smith, 1989,1990a,1991a). This study, in common with the other studies in Bolivia, was of a short duration encompassing the end of the dry season and the beginning of the rainy season. Buchanan-Smith (1990a) demonstrated that these primates maintained a high level of group cohesion, with each species being found within 50m of their congeners for 84% of the time. Over the study period the range size used by her main study group was almost identical for both species and they had very similar mean daily path lengths (Buchanan-Smith,1989). Her analysis of the data using Waser's (1987) formula, demonstrated that the association was not due to chance encounters and that the two species moved and behaved in a unified manner, whereby each species formed an association with only one group of congeners.

In addition to the 3 main studies of *S. labiatus* and *S. fuscicollis* in Bolivia, several other authors have noted the association between these monkeys (e.g. Cameron *et al.*, 1988; Christen & Geissmann, 1994; Encarnacion & Castro,1978; Freese *et al.*, 1982; Kolhaas,1991; Pennington *et al.*, 1988). In all cases where *S. labiatus* were observed, they were found to co-exist with *S. fuscicollis*, thus throughout the area where these species are sympatric (see Section 1.5) they form mixed-species groups.

Mixed groups of tamarins can be thought of as being an association of two species with both similarities and differences in terms of their ecology and life-style (see Chapter 1). The available studies show that *S. labiatus* and *S. fuscicollis* of northern Bolivia have similarities in terms of range size and ranging patterns, as well as consuming many of the same plant materials (e.g. Buchanan-Smith,1989; Yoneda,1981). There is a difference in terms of the vertical separation of the two species. Invariably, *S. labiatus* occupies a higher average height of the forest, with the absolute height being dependent upon local variants in forest height and type. These differences were most clearly manifest in locomotion, resting and insect foraging, where they differed in size class of prey taken (Yoneda,1981, 1984b; Pook & Pook,1982; Buchanan-Smith, 1989,1990a). The *S. labiatus* were found to take smaller prey items, which they gained through a visually directed "stalk and pounce" technique, while *S. fuscicollis* were shown to capture larger insects, near to the ground, and though probing in crevices for hidden prey (Yoneda,1981). Differences were also found in preferred locomotory style, where the *S. labiatus* were shown to locomote predominantly using quadrupedal walking and running, and leaping, while the *S. fuscicollis* often progressed through the lower areas of the forest, using vertical clinging and leaping (e.g. Pook & Pook, 1982).

2.1 Aim of present study.

The present study was carried out in an attempt to elucidate similarities and differences in the behaviour of these 2 primates in their natural habitat. As mentioned above, these species have not been previously subjected to any large scale observation, and there remains very little known about their ecology and behaviour in Bolivia. This is particularly pertinent in the case of *S. labiatus*, about whom little is known of its behaviour at any location. While the main focus of this study was concerned with attempting to learn as much as possible about the two species involved in mixed-species troops, it was also considered to be equally important to gain information about the behaviour of *S.labiatus*. Lastly, it was hoped to provide an opportunity to study the behaviour of these primates in an area of Pando more easterly than all the previous studies (e.g. Izawa & Bejarano, 1981; Yoneda, 1981,1984a,1984b; Pook & Pook, 1982, Buchanan-Smith, 1989), which were all concentrated close to, and mainly to the west of, Cobija.

2.2 Methodology & study area.

2.2.1 Location and background history of study site.

The main part of this study of *Saguinus fuscicollis weddelli* and *Saguinus labiatus labiatus* (Hershkovitz,1977) was carried out at two closely situated sites called "Bella Flor" and "La Garanja", located in the northwestern corner of Bolivia, in Province Nicholas Suarez of the remote Pando Department. These sites are some 140km east of Cobija, the Departmental capital, and are found at approximately 11°08'S, 67°48'W and 11°05'S, 67°50'W respectively.

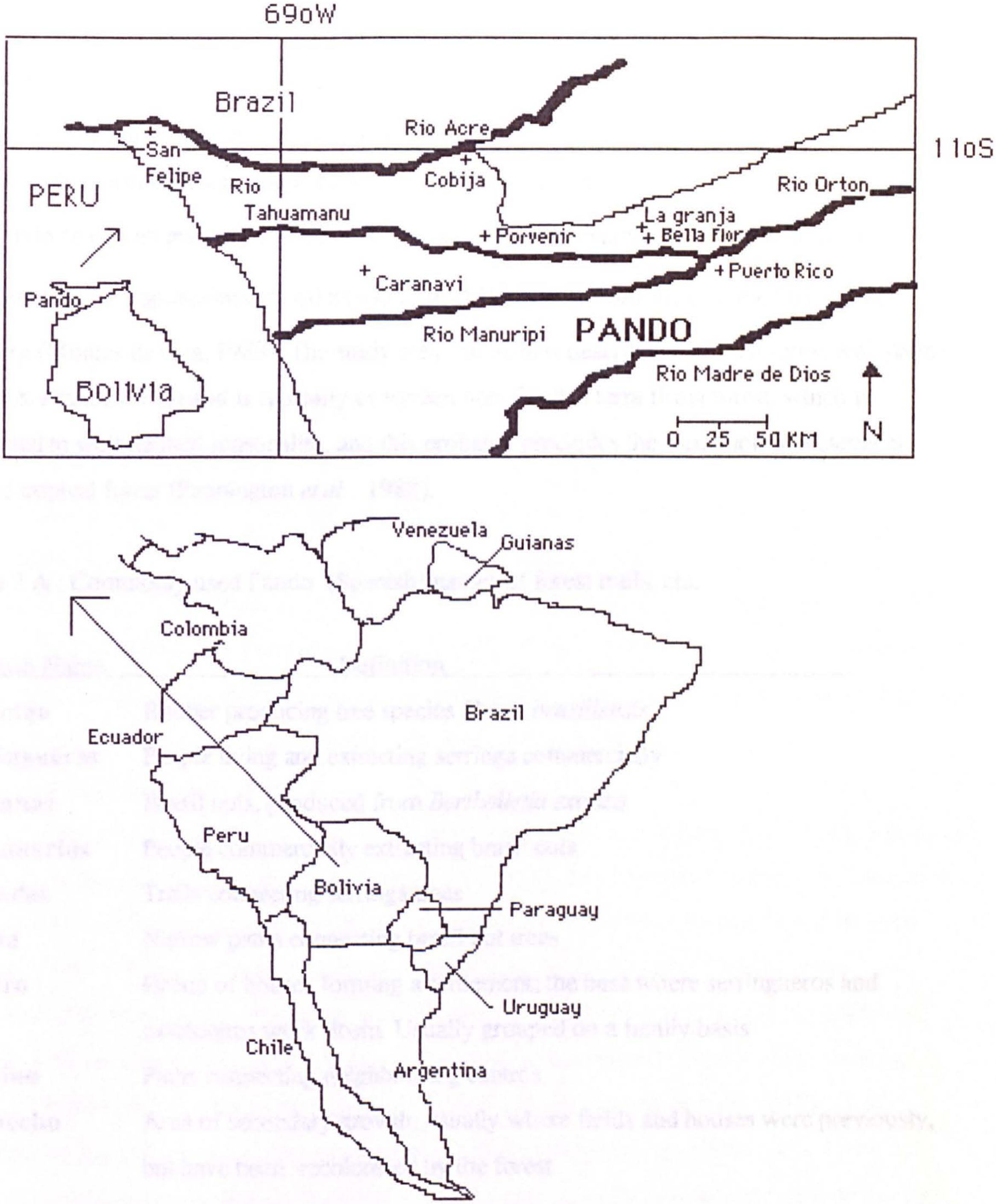


Figure 2.A : Location of study site (adapted from Morrison, 1985; Buchanan-Smith, 1989)

In addition, brief observations were also carried out at "San Felipe" near Rio Acre (10°58' S, 69°44'W) and at "Caranavi" in Manuripi Province (11°32'S, 68°42'W). The Pando forests form part of the Amazonian segment of Bolivian Forest (Cameron *et al.*,1988) and are bordered by Brazil, to the north and east, and Peru to the west. (Figure 2.A)

Pando covers an area of some 63,827 km^2 and is predominantly forested by "tropical evergreen forest" (approximately 60,816 km^2 in 1989), which constitutes some 90% of the territory (Montes de Oca, 1989). The study area can be best described as "open forest with palms" (Pires & Prance, 1985) and is typically evergreen non-flooded terra firma forest, which is subjected to well defined seasonality, and this probably precludes the formation of a classical closed tropical forest (Pennington *et al.*, 1988).

Table 2.A : Commonly used Pando (Spanish) names of forest trails, etc.

Spanish Name	Definition
Serringa	Rubber producing tree species *Hevea brasiliensis*
Serringueros	People living and extracting serringa commercially
Castanas	Brasil nuts, produced from *Bertholletia excelsa*
Castanerios	People commercially extracting brasil nuts
Estradas	Trails connecting serringa trees
Senda	Narrow paths connecting brasil nut trees
Centro	Group of houses forming a settlement; the base where serringueros and castaneiros work from. Usually grouped on a family basis
Camino	Paths connecting neighbouring centros
Barbecho	Area of secondary growth; usually where fields and houses were previously, but have been recolonised by the forest

The people of the forest are of a mixed European and Indigenous descent and generally practice a subsistence lifestyle that involves the commercial extraction of brasil nuts (castanas) and rubber (serringa) from the *Bertholletia excelsa* and *Hevea brasiliensis* trees respectively (Cameron & Buchanan-Smith, in press.) The exploitation of these natural products has led to a well defined system of paths connecting the trees of these species. Serringa trees are connected in long trails or "estradas", with approximately 100 or more in each estrada (For definitions of local names see Table 2.A). The route of the estrada follows the shortest distance between each tree encountered and generally follows a "meandering" pattern extending some 10-15 km (Pennington *et al.*, 1988). The study area contains one "centro"- in this case a group of two families that extract the serringa and gather castanas from the surrounding forest. Adjoining centros are connected by "caminos" and the brasil nut trees are connected by "sendas"- narrow pathways that are only cleared during castana season. Castanas are generally extracted from December until February, whereas serringa is extracted from May to December.

These paths provide a good basis for observing the monkeys and allow the observer to penetrate deeply into the forest. Although the forest used for this study cannot be described as primary forest in its strictest sense (Emmons & Feer,1991) it is basically mature forest with a fairly limited amount of human influence upon the distribution of plant species and as such will be considered to be "primary" for the purposes of this study. The schema has been adopted in previous studies of primates in Pando (Pook & Pook,1981; Yoneda, 1981,1984b; Izawa,1981; Buchanan-Smith,1989,1990a) and emphasises that this is essentially unspoiled forest, especially when compared to the heavily exploited secondary growth area (Barbecho) that appears after the forest has been cut for agriculture or housing. Excluding the gathering of castanas and serringa, the forest is basically intact and most original species are probably present.

2.2.2 Geography of study area.

The study area lies some 6km north of Rio Tahuamanu and is well drained by at least 3 streams (arroyos). This probably prevents the extensive flooding found only nearer to the river. The site is fairly flat, lies some 220m in altitude and as such is slightly higher than the main Amazon basin (Nichol,1990). The soil is categorised as "xanthic ferralsols" (FAO, 1971) but the exact composition varies visibly in certain areas of the site. All around the study area is relatively well preserved forest, although the area has been populated for the best part of 100 years, since the great "rubber-boom" of the late 19th and early 20th Centuries (Morrison *et al.*, 1985). The surrounding forest varies in quality and degree of human influence. Approximately 7 km to the north of the site passes the Cobija-Puerto Rico road; a two-lane dirt track which has large cleared areas adjacent to it, for crops and cattle. This may restrict the movement of animals to and from the study area, as well as leading to increased hunting pressure particularly upon the larger mammals. Further encroachment is expected as the road has recently been connected to the rest of Bolivia and a greater influx of settlers, ranchers and loggers is likely to follow.

2.2.3 Animal species encountered.

Primates

The forest is home to at least nine primate species (Table 2.B). In addition to the two *Saguinus* species being studied, the squirrel monkey (*Saimiri boliviensis*), night monkey (*Aotus* *trivirgatus*), red howler monkey (*Alouatta seniculus*), Grays' bald faced saki (*Pithecia irrorata*), Goeldis' monkey (*Callimico goeldii*), black capped capuchin (*Cebus apella*) and the dusky titi monkey (*Callicebus moloch*) are all known to occur. The black spider monkey (*Ateles paniscultus*) may occur but is hunted with such ferocity that it was not observed, although local people report it to occur in very limited numbers. The families living in the study area usually restrict hunting to the larger monkeys for meat (e.g. *Alouatta, Cebus* , *Callicebus, Pithecia*) but the other smaller monkeys (e.g. *Saguinus,Callimico* etc.) are free of these hunting pressures due to their small stature.

Table 2.B : Local names for primate species and scientific names (Local names in Spanish* or Portuguese**).

Scientific Name	Local Name	Common Name
Callitrichidae		
Saguinus fuscicollis	Leoncita*	Saddle-back tamarin
Saguinus labiatus	Monito boca blanca*	Red-bellied tamarin
Callimiconidae		
Callimico goeldii	Monito negro*	Goeldi's monkey
Cebidae		
Saimiri boliviensis	Amarillo*	Squirrel monkey
Alouatta seniculus	Manechi*	Red howler monkey
Callicebus moloch	Zogue-Zogue**	Dusky titi monkey
Pithecia irrorata	Macheno*	Grays' bald faced saki
Cebus albifrons	Silvadore*	Grey fronted capuchin
Cebus apella	Silvadore*	Black capped capuchin
Ateles paniscultus	Marimono*	Black spider monkey
Aotus trivigartus	Mono Nocturno*	Night monkey

Other mammals and birds.

A diverse mammalian fauna exists in the area but is substantially affected by hunting. A number of animals that were probably found previously in large numbers, may now be locally extinct. These include tapir (*Tapirus brasiliensis*), peccaries (*Tyassu spp.*) and the larger felids (jaguar- *Felis onca,* ocelot - *Felis paradalis*). These felids may still occur in small numbers as local people occasionally report seeing "tigres"- but whether they are ocelots or jaguars is unclear and numbers are probably minimal. A number of potential mammalian predators of tamarins are known to still inhabit the study area (e.g. tayras ; *Eira barbara* and jagarundis ; *Felis* *yagouaroundi*), and there is a wide range of potential aerial predators as well. These include the slate coloured hawk (*Leucopterus schitaceas*), the great black hawk (*Buteogallus urubitinga*), and the ornate hawk-eagle (*Spizaetus ornatus*). Snakes were infrequently observed but may be a danger as they are known to prey on tamarins (Bartecki & Heymann,1987). Overall, as aerial predators were most often encountered, they probably constitute the greatest danger, in terms of attack potential. Terrestrial predators were infrequently encountered, but this may be a factor influenced by the presence of the observer.

2.2.4 Forest details.

In order to get a more accurate picture of the forest it was decided to measure the canopy height, the size of emergent trees and the size of palms (as mentioned previously, a common plant type in this forest). A clinometer was used to estimate heights and the trees were randomly selected from areas throughout the study area.

As mentioned above, the main forest type in the study area was considered to be primary and was made up principally of trees of the *Moraceae* family. A main canopy was clearly apparent, where the majority of trees reached a similar height. This was interspersed with trees of a larger stature than the average canopy and these are referred to as emergents. The mean canopy height was in the region of 25-30m. Randomly selected emergents were measured and had a range of height between 33 and 48m (N = 46, mean height of 38.7m, S.E. = 0.63). The most commonly encountered species of emergents included : *Hevea brasiliensis, Dialium guianse, Castilla ulei, Chorisia speciosa* and *Inga* sp. Palms were also measured as they were an important part of the forest, a major constituent of the understory area and previous studies of tamarins indicated that *Saguinus fuscicollis*, in particular, may be found to use this area to forage and travel in (e.g. Yoneda,1984b).The height of randomly selected palms,were measured using a clinometer and had a mean height of 12.5 m (N = 15, range 6.5 - 17m. S.E. = 0.9).

2.2.5 Climatic details.

The weather conditions of the study area were measured during the course of the study. Temperature was measured (maximum and minimum) day and night and all rainfall was recorded. Ranges of temperature and amount of rain per month are shown in Table 2.C. A clear dry season occurs from May until September (cf. Buchanan-Smith, 1989) and in terms of rainfall the area lies below the level of 2000 mm per year (Pennington *et al.*, 1988).

Table 2.C : Temperature and rain in Bella Flor (August & September) and La Garanja (October-December 1991).

Month	Temperature range	Mean Temp.	Rainfall
August	: Night 14°C-22.5°C	18.4°C	<10mm (3 days)
	: Day 36°C-39°C	37.1°C	
September	: Night 18°C-23°C	20.5°C	134mm (10 days)
	: Day 21.5°C-38°C	32.5°C	
October	: Night 14°C-23°C	19.9°C	96mm (11 days)
	: Day 24.5°C-39°C	33.2°C	
November	: Night 15°C-32°C	23.5°C	169mm (7 days)
	: Day 32°C-39°C	35.2°C	
December	: Night 20°C-26°C	22.4°C	238mm (14 days)
	: Day 28°C-37°C	32.9°C	

2.3 Sampling methodology.

The study was carried out from June until December 1991 and therefore covers most of the dry season and the beginning of the rainy season. Observations were not carried out over the full time period, as trips to the capital La Paz, were necessary for the identification of botanical samples and for provisions.

When tamarins were opportunistically encountered in the forest, during the process of trying to trap them for radio-tracking, an attempt was made to record the following data on the first individual of the tamarin species encountered :

1) Height in Forest (in categories 0-5m, 5-10m etc.)
2) Activity (put into mutually exclusive categories; see Table 2.D)
3) Angle of Substrate Used (Horizontal 0-15°, Oblique 16-74°, Vertical 75-90° ; deviations from horizontal axis : see Garber, 1984b)
4) Size of Substrate Used (Diameter ; Small<5cm, Medium 5-10cm,Large 10cm+ : see Garber, 1984b)
5) Posture of Animal (see Table 2.E)
6) Comments

If more than one individual was in sight, an attempt was made to record the same data for every subject (i.e. a scan sample technique; Martin & Bateson,1986), provided that the animals did not obviously change activity etc., due to the presence of the observer. This was, however, very difficult as the animals were not habituated to the presence of the observer. Also due to the small size of the monkeys, combined with their height in forest and dense vegetation, it was often very difficult to observe them.

Upon coming across a group of tamarins, an estimate of group size was attempted. It was only assumed to be reliable if the animals were clearly observed, i.e. crossing a gap in the canopy. Also, if the same count was obtained for a group, for two or more sightings (in the same vicinity) it was assumed this count was accurate. The presence or absence of congeners (i.e. other *Saguinus* species) was noted.

Table 2.D : Mutually exclusive behavioural categories used to define activity of tamarins (Based on Buchanan-Smith,1989; Coates & Poole, 1983; Garber, 1980a,b, 1984; Price, 1990a).

Behaviour	Definition
Look	Animals is in a stationary position, with scanning head movements (in both vertical and horizontal planes), or fixation of stare on object or animal
Insect Feed	Animal searches, by manipulating substrates or by visual inspection, through the area to gain an insect food item (forages) and/or consumes an insect
Fruit Feed	Animal searches by manipulating substrates, through the area to gain a plant food item (forages) and /or consumes fruit
Rest	Stay still and relaxed in any posture (does not include any other categories, e.g. groom, huddle etc.)
Huddle	Stationary contact with another, where torso and/or limbs are touching (does not include any other behaviour)
Groom	Individual picks through hair of another, with visual inspection and parting of the hair by hand(s) or mouth, or self grooms
Play	Racing and acrobatic movements chasing or being chased, wrestling, rough-and-tumble and "mock" biting
Locomotion	All movements (except play) in which the body is displaced relative to its surroundings
Alarm call	Animal calls out and acts in an alarmed manner, different from other calls
Other	Any behavioural pattern not otherwise listed (e.g. copulations, nursing infants, etc)

Table 2.E : Mutually exclusive categories of positional behaviour, used for tamarins (After Garber, 1980a,b, 1984, 1991).

Position	Definition
Sit	Squat with hind limbs or all four limbs resting on the substrate
Quadrupedal Walk	Move forward with alternating movements of limbs with the contralateral fore and hind limbs simultaneously making contact with the substrate
Q. Run	As quadrupedal walk, but using a faster gait
Ascend	Move diagonally or vertically to a higher position than starting point. Separated from Q.Walk by the animal using a prehensile hold on substrate
Descend	Move diagonally or vertically to a lower position than starting point, either head first or tail first. Again separated from Q.Walk by the monkey gripping substrate with its limbs
Bipedal Suspend	Hang supported by fore- or Hind-limbs, with hands or feet gripping
Quadrupedal Suspend	Hang supported by all four limbs, with hands and feet gripping prehensively. This includes suspension by three limbs while manipulating an object
Leap	As colloquial use, e.g. jump
Lie	Recline on substrate, either on back, front or side, with no weight on limbs
Vertical cling & Leap	A form of locomotion between large vertically orientated substrates, involves quadrupedal suspension, and leaping between the supports (see Garber,1991)
Other	Any other position

If the other species was in sight of the observer at the same time as the initially observed species (i.e. usually within a distance of 20-40m), this was classed as the two species being in association. This was a somewhat arbitrary definition of association, but represented the limits of my field of vision in the study area. These details were noted, as were details of group size and other monkey species present; all were recorded ad libitum. Subsequent data was collected at two minute intervals, while the monkeys were in view.

All instances of fruit and insect feeding and any interaction between the species was noted ad libitum, when they occurred during chance encounters. Where possible, samples of foliage and fruits of plant species consumed by the monkeys were collected for formal identification at the Herbario Nacional de Bolivia, in La Paz. Leaves and flowers were pressed in newspaper, while fruits were stored in alcohol. This allowed them to be preserved for future identification.

The original intention was to capture a group of tamarins and to radio-collar two or more individuals of each species. The method used was basically the "trampa Saguinus" method (Encarnacion *et al.*,1978) and proved to be unsuccessful. Initially the tamarins had to learn to consume bananas (the chosen incentive to enter the trap)- a fruit not native to the area. This involved tying 2 or 3 ripe yellow bananas onto 3-6 trees, at a height of 2m or more. The chosen sites were near to fruiting trees and/or on travel paths used by the tamarins. This process of introducing wild tamarins to bananas involved a calling animal - a "pet" *S. labiatus* being kept in a small cage (approximately 30cm X 30cm X 30cm). This cage contained a single perch and the bottom was sealed to prevent the animals' long tail from protruding. The calling monkey was suspended amongst the bananas at a height of approximately 2m.

The initial step was to place the calling monkey in the trees and for the observer to hide a short distance away. At different localities, the process lasted a few days to a few weeks and was often not successful. Where the wild groups approached the calling animal, they often ignored the bananas; other times they ate for one day, but failed to return on other days. A criterion of three days consumption of bananas was set before the trap was installed at a location. Once this was reached, the trap was installed at a height of 1.5m . The trap was the same one used by Buchanan-Smith (1989) and consisted of 12 compartments 20cm X 12cm X 40cm, each with a door hinged at the bottom. Strings were attached to each door and they led to a hide which was situated some 6m from the trap. Each compartment was baited with a banana, while the calling monkey was held in its small cage near to the trap to attract the tamarins to the trapping area.

On two occasions *S. labiatus* were attracted to the site and showed great interest in the calling monkey. They were, however, very nervous and did <u>not</u> enter the trap, although they showed a great interest in the bananas. As no animals would enter the trap, it was not possible to capture them.

The two main reasons contributing to the failure to catch monkeys were probably the timing (due to rainy season) and the event of birth of infants. For example, arrival of the rainy season brought a profusion of fruits within the forest, thus giving the monkeys plenty of alternative foods perhaps making the bananas not a very attractive alternative. On the other hand, the birth of infants may have led to the monkeys being more cautious and it was therefore not surprising they did not enter the "strange" traps and /or consume the unknown bananas.

The study was prematurely terminated in December 1991, due to illness, and most of the available time was spent trying to capture the animals and not trying to observe them.Therefore only a limited amount of time was available to spend on observation of the monkeys.

2.4 Statistical analysis.

Due to the small number of observations, normality of distribution of results could not be assumed and therefore non-parametric statistics were necessary (Siegel & Castellan, 1988). Kolmorogov-Smirnov and Chi-Square statistical analyses were used and significance was set at $p<0.05$.

2.5 Results.

Although over 300 hours were spent in potential observation time in the forest, much of this period was spent with the observer out of sight of the animals, in the preparation of sites and equipment, in an attempt to trap the animals. This means that they do not represent time spent walking trials, or any direct transect methods, and therefore observations were generally of an opportunistic nature and for the most part, only occurred when animals were encountered during the trapping process.

2.5.1 Primates inhabiting the study area.

In terms of diversity, there were at least nine species of primates present in the study area, with the two tamarin species being encountered most often. Two other sites, visited for a short period, yielded different combinations of species, although one of them, San Felipe, had numerically as many distinct species present (Table 2.F).

Table 2.F : Species of monkeys encountered at three sites in Pando.

	San Felipe[1]	Bella Flor[2]	Caranavi[3]
Saguinus labiatus	*Observed*	*Observed*	
Saguinus fuscicollis	*Observed*	*Observed*	*Observed*
Cebus apella	*Observed*	*Observed*	
Cebus albifrons	*Observed*		
Pithecia irrorata	*Observed*	*Observed*	
Saimiri boliviensis		*Observed,*	*Observed*
Aotus trivigartus	*Heard*	*Heard*	
Callicebus moloch	*Observed*	*Observed*	*Observed*
Alouatta seniculus	*Heard*	*Observed*	
Callimico goeldii	*Observed*	*Observed*	

Locations			
	1) **San Felipe**	:	Rio Acre (one week) ; 10°58'S, 69°44'W (30 hours observation)
	2) **Bella Flor**	:	Nicholas Suarez (two months) ; 11°08'S, 67°48'W (100+ hours obs.)
	& La Garanja	:	Rio Tahuamanu (three months) ; 11°05'S, 67°50'W (200+ hours obs.)
	3) **Caranavi**	:	Manuripi Province (two days) ; 11°32'S, 68°42'W (12 hours obs.)

Most species were encountered infrequently, often only on 1, 2 or 3 occasions (*Cebus apella, Cebus albifrons, Saimiri boliviensis*). *Callicebus moloch* were encountered on 4 occasions at Bella Flor and twice at Caranavi. Each time they were encountered in pairs (5 occasions) or trios (once) but never with other species. *Pithecia irrorata* were observed on 6 occasions, with 2 individuals present during 5 occasions, and 3 individuals present in the remaining encounter. *Callimico goeldii* were found at both San Felipe (1 group of at least 3 individuals) and around Bella Flor. At least 4 groups of *C.goeldii* were observed within a radius of approximately 5 km of Bella Flor and contained at least 2 (N= 3) or 3 (N=1) individuals. All 4 groups were encountered 1km or more from each other and were considered to be distinct groups.

2.5.2 Encounters with mixed-species groups.

An indication of the occurrence of mixed-species associations of tamarins within the population in general, was determined from the observations of polyspecific and monospecific groups. Only observations in which the observer was sure of the presence/absence of congeners (i.e. within close (<40m) visual and/or auditory contact) were included. This gave an indication that for some 75% of the time the two species were encountered together. The data reveal that 88% of all sightings of *S. fuscicollis* and 83% of sightings of *S. labiatus* were in mixed-species groups (Table 2.G). This can be seen as a minimal estimate and the general impression was that most or all of the study area was populated by territories containing both species.

Table 2.G : Occurrence of polyspecific and monospecific *Saguinus* groups, where only unambiguous sightings were used. Data pooled from all sites, 300+ hours of observation.

	Number of groups	Per cent of observations
S. fuscicollis & S. labiatus	29	75%
S. fuscicollis only	4	10%
S. labiatus only	6	15%

In addition, on 5 of the 6 occasions *Pithecia irrorata* were observed, they were in close proximity (<20m) to the tamarins (1 or both species). In all cases the *P.irrorata* were consuming the same plant materials (e.g. *Ochroma lagopus, Clarisia racemosa*) as the tamarins. No integrated movement with the *Saguinus* species was observed, and these encounters were best described as being only "chance" encounters (Waser,1982).

Callimico goeldii were observed very rarely (6 occasions), but each time they were found within 20-40m of one or both tamarin species (N=2 with *S. labiatus* only; N=4 with both species). Due to the great shyness of these monkeys, they were never observed for more than 5 or

10 seconds and so were not shown to form associations in the same manner as the *Saguinus* species.

2.5.3 Group size of tamarins.

From all "good" counts (where the observer was sure of numbers) of group size, it was possible to calculate an average group size for both species. These estimates are thought to be accurate, due to the criterion used (i.e. only "good" counts). Infants being carried by a group member during the observation were included in the counts. The average group size of *Saguinus labiatus* was larger than that of *Saguinus fuscicollis* . On a subjective level, more groups of *Saguinus labiatus* were generally seen and they were usually of a greater size than *S. fuscicollis* groups (Table 2.H). Single individuals for either species were not encountered during the course of the study.

Table 2.H : Group size of *Saguinus* groups at Bella Flor & La Garanja, Bolivia.

A) "Good" Observations

	Group Size									Mean Size
	3	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	
S. labiatus	-	1	2	6	1	2	1	1	1	**6.1**
S. fuscicollis	1	2	2	2	2	2	-	-	-	**5.7**

B) Summary of Data

	Number of Groups	Number of Individuals	Mean Group Size
Saguinus labiatus	15	4 - 11	6.1
Saguinus fuscicollis	11	3 - 8	5.7

2.5.4 Birth of infants.

Single infants were first observed for *S. labiatus* from September onwards in 3 or more groups, throughout the study site. In October one group of *S. fuscicollis* was observed to carry one infant, and two further groups carrying single infants were encountered in November. Also, in the previous June one group of *S. fuscicollis* was seen to carry an infant of approximately 2 months of age. This is suggestive, albeit mildly, of some seasonality in births ; with births for both species centred at least around the period August - November . In the case of *S. fuscicollis* they may have year round birth period, but probably most births are centred around the beginning of the wet season, when fruit is abundant. For both species not enough observations were taken to provide support for birth seasonality.

2.5.5 Sleeping tree.

On one occasion the observer saw a group of *S. labiatus* leaving a tree that was likely to have been their sleeping site for the previous night. As the observer was present before daybreak and saw no movement prior to this observation, it is assumed this was the site where they stayed overnight. The site was located at La garanja, in a serringa tree (*Bertholletia excelsa*), some 22 metres tall, where the tamarins emerged out of a hole at the top. The crown of the tree had been split off the top, probably in a storm, and this left an entrance for the monkeys at the top. There were numerous lianas and epiphytes near to the hole, thus providing cover for the monkeys. Palms and other tees were adjacent to the sleep site, thus allowing "safe" entry and exit from the tree. The local serringueiros reported seeing the *S. labiatus* leaving the tree early in the morning, on "many" occasions.

2.6 The use of plant material.

Table 2.I shows the plant material which both species of tamarins were observed to consume and gives the scientific names as determined by Dr. Stephan Beck of the Herbario Nacional de Bolivia. The "availability" was determined from my estimate of abundance of each resource used, and represents a minimal estimate of when the resources were present in the study area and therefore must be viewed with caution. The "eaten by" category contains the identity of whichever species of tamarin was observed to consume the plant material, but again must be viewed with caution, as they may involve only single observations of the tamarins using the resource. Clearly not all types of plant material were utilised by both species of tamarin. Nevertheless, the observations give the picture of at least a 63% (10/16 plant species) overlap of observed plant resources, between the 2 tamarin species.

Of the 6 species of plant material not seen to be shared by the tamarins, 4 species were used only by *S. labiatus* and 2 species used only by *S. fuscicollis* (see Table 2.J). If we examine certain characteristics of the plant resources, some trends occur. The main factor that can be drawn from the shared resources is that *S. labiatus* appeared to feed first on the resource, and typically most or all of the *S. labiatus* leave the feeding tree before the *S. fuscicollis* enter the feeding tree (Table 2.J). This means that the monkeys usually fed in a serial manner, i.e. one species after the other.

Table 2.I : Identification and characteristics of plant species consumed by tamarins.

Scientific Name	Family	Type	Eats	Size	*Available	*Eaten by
Chorisia speciosa	Bombacaceae	Tree	Flower Fruit	<5cm <15cm	May,June June,July	S.f S.lab
Ochroma lagopus sw	Bombacaceae	Tree	Flower	10cm	May-July	S.f
Celtis sp.	Ulmaceae	Liana	Fruit	1.5x1cm	June,July	S.f
Cassia sp.	Leguminoseae	Tree	Fruit	1 x 4cm	July	S.lab
Clarisia racemosa	Moraceae	Tree	Fruit	2.5 x1.2cm	June- Sept	S.lab
Dialium guianse	Leguminoseae	Tree	Fruit	0.8 x 1.5cm	July	S.lab,S.f
Pseudolmedia sp.	Moraceae	Tree	Fruit	1.5 x 1cm	Aug.,Nov.	S.lab,S.f
Cercropia sciadophylla	Moraceae	Tree	Fruit	8-20 x 1-2cm	Aug-Oct.	S.lab,S.f
Inga sp.	Leguminoseae	Tree	Fruit	3-18 x 1-1.5cm	Aug-Oct	S.lab,S.f
Brosmium guianensis	Moraceae	Tree	Fruit	2 x 1.6cm	Sept,Oct	S.lab,S.f
Pourouma guiansis	Moraceae	Tree	Fruit	2 x 1 cm	Oct,Nov	S.lab,S.f
Brosmium lactescens	Moraceae	Tree	Fruit	1.4 x 1.3cm	Oct,Nov	S.lab,S.f
Local Names Only						
"Manzanillo"	Solanaceae?	Tree	Fruit	1.8 x 0.5cm	August	S.lab
"Paquio"	Leguminoseae	Tree	Flower	<0.5cm	August	S.lab
"Verdolago"	Combretacea	Tree	Fruit	1.5 x 2 cm	September	S.lab,S.f
"Colordillo"	?	Tree	Fruit	1.6 x 1 cm	September	S.lab,S.f

Table 2.J : Characteristics of plant species used by Bolivian tamarins.

A) Used by both species

Chorisia speciosa	*S. labiatus* (fruit) then *S. fuscicollis* (flower) Large crown (>20m) Few (<50) flowers, Few (<50) fruits
Dialium guianense	*S. labiatus* then *S. fuscicollis* Large crown (>10m) Large amount of fruit (100+)
Pseudolmedia sp.	*S. labiatus* then *S. fuscicollis* Medium crown (< 10m) Large amount of fruit
"Coloradillo"	*S. labiatus* then *S. fuscicollis* (but overlap last S.l and 1st S.f) Small crown (<5m) Little fruit (<50)

Cercropia sciadophylla	*S. labiatus* then *S. fuscicollis* Medium crown (<10m) Medium level of fruits (50-100)
Pourouma sp.	*S. labiatus* then *S. fuscicollis* Medium crown (5-10m) Large amount of fruit (100+)
Inga sp.	*S. labiatus* then *S. fuscicollis* Large crown (>10m) Large amount of fruit (100+)
Brosmium lactescens	Both species consume fruit, but observed when "solo" Large crown (>10m) large amount of fruit (100+)
Brosmium guianensis	*S. labiatus* then *S. fuscicollis* large crown (>10m) Large amount of fruit (100+)
"Verdolago"	*S. labiatus* then *S. fuscicollis* Medium crown (<10m) Medium amount of fruit (<100)

B) Used by *Saguinus labiatus* only

Clarisia racemosa	Large tree (30m+) Large canopy (>10m) Large amount of fruit (100+)
"Paquio"	Large tree (30-35m) Large canopy (>20m) Large amount of fruit ("buds") (100+)
Cassia sp.	Large tree (30m+) Large canopy (20m) Large amount of fruit (100+)
"Manzanillo"	Large tree (30m) Medium / Large canopy (10m) Medium amount of fruit (<100)

C) Used by *Saguinus fuscicollis* only

Celtis sp.	Liana; small (10-15m) Crown medium sized Large amount of fruit (100+)
Ochroma lagopus	Small tree (10-15m) Crown small (<5m) Few fruits (<50)

Notes

Although there often was a large amount of fruit, there generally was only a small number of fruits at full ripeness at any one period.

Size:	Large crown 10m +	**Fruits**:	Few fruits (<50) Items ripe & unripe fruit
	Medium crown 5-10m		Medium amount of fruits (50-100) items
	Small crown < 5m		Large amount of fruit (100+) items

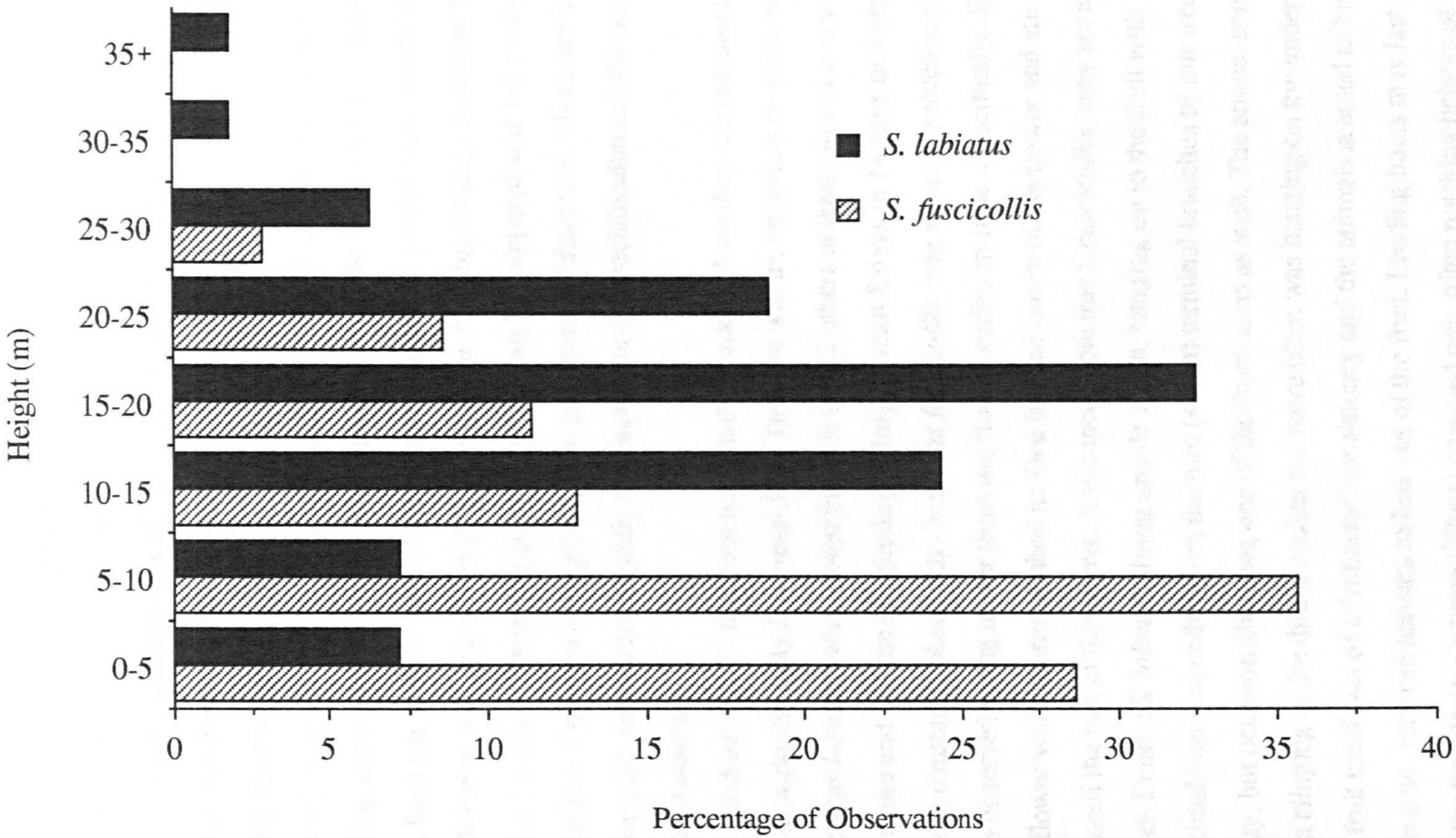


Figure 2.B : Height utilisation of forest by tamarins in northern Bolivia, for all activities, (For S.labiatus N= 111, mean 16.3m ; For S.fuscicollis N= 70, mean = 9.7m : Kolmogorov-Smirnov D = 0.5, m=111, n=70, $p<0.001$).

In terms of tree species exploited by *S. labiatus* only, it appears that they were all medium-large crowned tall trees, often emergents. In contrast the 2 species only eaten by *S. fuscicollis* were small trees. This fits in with the vertical partitioning of the forest shown by the 2 species (see Figure 2.B), whereby *S. labiatus* usually occupy a higher area of the forest than *S. fuscicollis.* Due to the small numbers of feeding trees observed and the short duration of the study, this must again be viewed with caution.

2.6.1 Foraging methods of tamarins.

A number of plant food resources were discovered through opportunistic encounters with tamarins feeding, and by following animals moving through the forest until they began to eat from feeding trees. Looking at the nature of the resources used it is possible to examine these resources in a slightly different way, one which is based upon the foraging strategy needed to harvest them. Observations of tamarins consuming plant materials can be compared with the method needed to extract the resource. Common strategies used to gain items of food from plants are manifest on a variety of plant types and are presumably representative of specialisations on the part of tamarins to exploit these resources.

Chorisia speciosa Sf hil. : fruits are harvested at a stage where they are immature. Availability of the fruit was approximately June until July. The fruit was an important resource to at least one group of *Saguinus labiatus* who visited this tree (and 2 others at least) almost every day in a 2 week period at the end of June / beginning of July (at least 8 days in 14 days of watching; where the tree was not constantly observed). *Saguinus fuscicollis* was never observed to eat from this fruit, but was observed eating nectar from the flower, earlier in June. Specifically, *S. fuscicollis* grabbed the flower with an arm, pushed its face into the centre of the flower and ate from the centre. It ignored the rest of the flower. It is conceivable that *S.fuscicollis* may act as a pollinator for this flower. **Fruit** ; *S. labiatus* hung upside-down, hanging on to the fruit with 1 or both front arms. The animal was suspended from the thin (<5cm) terminal branches of this tree, usually by back legs only, but occasionally using one of the front arms as well. The animal sometimes was upright when clinging to the thin branches but more often was hanging on the underside of the branch. The fruit itself was of a "rubbery" consistency and the animals seemed to be biting at the outside of the fruit. Exudate appears to leak out of the fruit. Feeding bouts may last five or more minutes and the tree itself is a large (20m+) crowned tree, often reaching heights of 40 metres or more.

Ochroma lagopus : These are large (10-15cm) flowers of the *Bombacaceae* family, which appear from May until July. *Saguinus fuscicollis* were observed to eat from the centre of this flower, in a manner similar to that for *C. speciosa.*

Celtis species : these are small fruits (<1cm) of a liana and they are basically eaten in the same manner as Terborgh (1983) describes for *Celtis iguanea.* These drupes are found on the liana, are split open in the monkeys' mouth, the slightly tough exocarp is then ejected as the animal chews on the "sweet mucilaginous" coating around the large central seed. The seed may be ejected but is more often swallowed. This species was used during June and July. Only *S. fuscicollis* was observed eating this fruit. "Verdolago" was consumed in a similar manner, and the single seed was also ejected.

Dialium guianense (Aubl.) Sandw.: was consumed in a similar manner to *Celtis* but this species contains 2 seeds. It was consumed by both the species of tamarin, during July (at the very least).

Clarisia racemosa Ruiz et Pav.: Only *S. labiatus* were spotted eating these fruits in this large (30m+) tree. Fruits were orange (became redder as they matured), oval shaped with a fairly thick outer skin. Two, three or more berries hung in a "grape like" bunch. The monkeys grabbed the fruit in their hands, with the body usually in an upright position (i.e. not upside down), making use of the back legs (and often one of the arms), to gain a grip on the substrate. These fruits were often found on more sturdy branches than *C. speciosa*, hence the upright stance while harvesting these fruits. The *S. labiatus* ate the outside part of the fruit, while it was still on the tree, not spending much time (<10 secs) at each drupe, but visiting many drupes.

Pseudolmedia sp ; Again the seed coating was consumed, the skin being ejected, along with the seed sometimes. The animal clung (using between 2 and 4 limbs) to the obliquely and vertically orientated branches, picking the fruit with the hands or mouth. Suspension was either upright or upside down, depending upon branch thinness, etc. Eaten by both species. "Manzanillo" and "Colordillo" were also eaten in a similar manner.

Cecropia sciadophylla Mart. : The fruits of this species generally hang downwards from the reasonably thick branches (med-large), that are necessary to support the large light-gathering leaves of the plant. The animal clings on to the branch, using 3 or 4 limbs for support, whilst manipulating the fruit with the mouth and/or the hand. The structure of this plant allowed this strategy and the angle of the body of the monkey (i.e. whether orientated upside down or upright) depended on the exact location of the fruit. Both species consumed this plant.

Inga sp. : This fruit of the *Leguminoseae* family, is a "pod" fruit, with fleshy covered seeds being found inside. The fruits were found hanging down from mainly thin branches. This in effect meant that the tamarins (both species) had to suspend their bodies from these branches whilst manipulating the fruit. The seeds usually appeared to be consumed, especially by *S. labiatus*, but this is not clear. On at least one occasion while on a thicker branch, a monkey was observed to reach down and grab a pod and eat it while sitting on the branch.

Brosmium lactescens (S.Moore) C.C.Berg & Brosmium guianense (Aubl.) Hub. ex Ducke :

Both these species were found in the same area and they are closely related in form and taste. The two species of tamarins consumed these fruits eating the seed, its coating and much of the skin in the attempt. Fruit is generally found on the terminal ends of thin obliquely and horizontally angled branches. Thus the most efficient and productive way to handle the fruits is the "grasping strategies" mentioned before. The monkeys usually hung by their back legs and manipulated the fruit with hands and mouth, or where necessary, used the additional support of the arms to hold-on, leaving the mouth free to harvest the fruits. Also, this strategy was used for *Pourouma guianensis.* In addition, although *Cassia* and "Paquio" were not observed clearly, their fruits were found on the terminal ends of branches, where grasping strategies were required to harvest them.

In summary, it is true to say that during the observation period fruit was most commonly taken from the thin (<5cm) terminal branches of trees. The actual size of the branches and fruits, and their position on the branch were an important factor, but usually extraction of fruit was heavily reliant upon "grasping strategies", with oral and / or manual manipulation being utilised to extract these fruits. Seeds were frequently swallowed along with the fruits. Many of these resources occurred on thin terminal branches, and were seen to have ripening patterns whereby only a small amount of ripe fruit appeared at any one point in time. This may have allowed the tamarins to exploit food resources not available in sufficient amounts to larger animals, particularly other primates. Tentative evidence for this is provided by the lack of observations of tamarins eating these fruits concurrently with other primates, and the thinness of these branches probably excludes competitors by their larger body size being physically prohibitive.

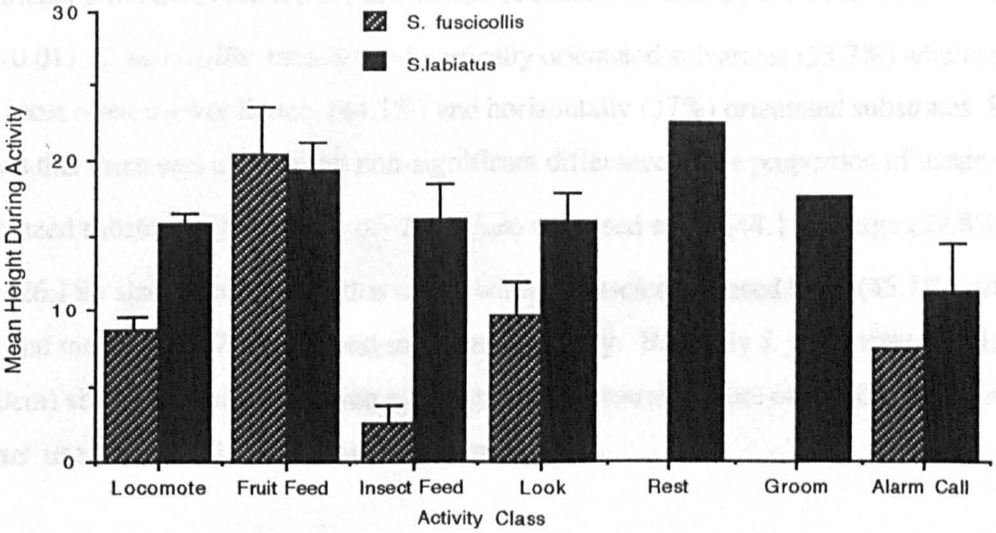
2.7 Activity budgeting and height preferences.

When comparing the 2 species over all activities it soon became apparent that there was a different level of forest used by both species. Overall there was a significant difference between the 2 species, where they did not use the same parts of the forest, or use them to the same degree (Kolmorogov-Smirnov $D_{m,n}$= 0.5, m =111, n=70, p<0.001). More specifically *S. labiatus* occupied a higher average level of forest than *S. fuscicollis,* with a mean height of 16.3m compared to a mean of 9.7m (Figure 2.B). This difference was large and was, for example, most pronounced in the 0-10m area, where *S. fuscicollis* was found there for over 64% of the time but *S. labiatus* was there for only about 15% of the time. Conversely, in the region of 20m and above, *S. labiatus* was present for 29% of the time, while *S. fuscicollis* was never observed (at least during observation periods) in the 30m+ height category. The data clearly shows a preference for the middle and lower canopy areas in both species (i.e. <20m: for *S. labiatus* 71% of the time, *S. fuscicollis* 89% of the time).

Originally it was hoped to gain enough data to compare activity budgets of the 2 species and to construct a profile of where (in terms of height in forest) specific behaviours occurred. Unfortunately this was not possible due to paucity of data but there was still enough data to compare the species on a more general basis (Table 2.K). It was evident that locomotion was the most commonly observed behaviour for both species. So consequently the difference in mean height used during locomotion, is probably the most robust comparison due to its larger number of observations. Therefore locomotion will be investigated in more detail later on.

Table 2.K : Average heights of forest utilised by two species of Bolivian tamarins, during various activities. [Means were calculated from the mid-points of each height category].

	Saguinus fuscicollis	***Saguinus labiatus***
Locomote	8.7m (N = 49,SE = 0.81, range 0.1-25m)	15.7m (N = 62,SE = 0.79, range 0.1-30m)
Fruit Feed	20.3m (N= 7, SE = 3.25, range 0.1-30m)	19.3m (N = 19, SE =1.72, range 0.1-35m)
Insect Feed	2.5m (N = 3, range 0.1-5m)	16 m (N = 10, SE = 2.36, range 0.1-30m)
Look	9.7m (N = 9, SE=2.22, range 0.1-25m)	15.9m (N =13, SE = 1.89, range 5-35m)
Rest		22.5m (N = 1)
Groom		17.5m (N = 2)
Alarm Call	7.5m (N=2)	11.3m (N =4, SE = 3.15, range 0.1-20m)

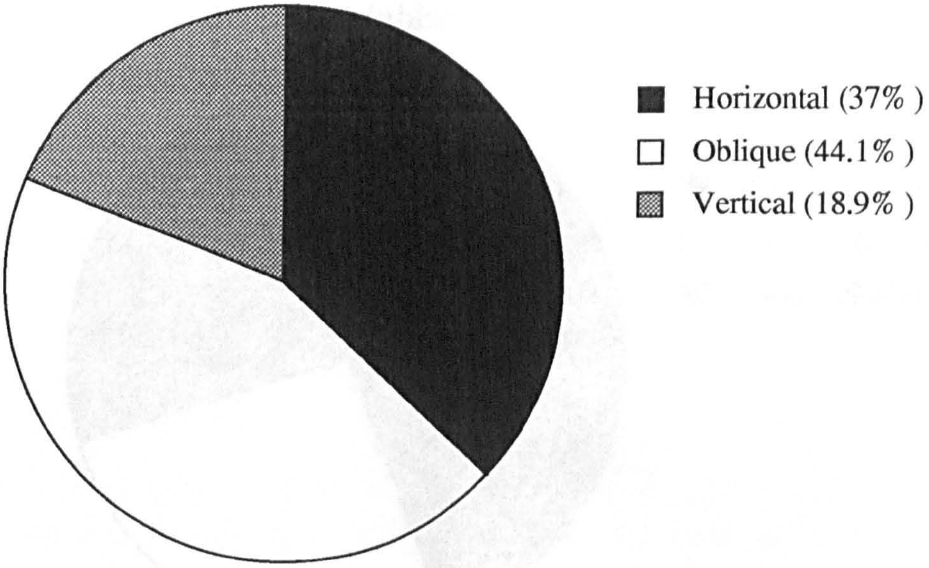


From the observations gained during encounters with tamarins, the 3 main activities observed were, locomotion, insect foraging, and fruit feeding. The mean height used by *S. labiatus* was mostly higher than that for *S. fuscicollis* (i.e. for 4/5 activities that were recorded for both species). The fruit feeding was carried out at a similar height ; which is not surprising considering the considerable overlap of fruit species consumed by the 2 species (see Table 2.I). These results correspond with the observers' general impression ; *S. labiatus* were usually observed higher in the canopy than *S. fuscicollis*, except when consuming and/ or foraging for, commonly used fruits.

The difference in insect foraging was almost certainly due to the difference in foraging styles used by the 2 species. *S. fuscicollis* used a manipulative, extractive style, whereby they inserted their fingers into gaps and holes in tree trunks and at the apical shoot area of palms.They did catch the occasional flying/ moving insect but this was much more infrequent than for *S. labiatus*. They used a "seize and capture" technique, where they lifted leaves, looked at the underside and generally tried to capture any moving or resting insects that they disturbed. They also kept watch, and caught any insects that they observed moving and/or roosting on foliage. This by the nature of the activity took place high in the thin leave covered branches and allowed the 2 species generally <u>not</u> to overlap in the height at which they consumed insects.

In order to further examine the differences in height usage, the orientation and size of substrate used by the tamarins was compared (Figures 2.C and 2.D). From Figure 2.C it is clear that there is a significant difference between the orientation of substrates used by the tamarins ($x^2 = 26.95$, df=2, $p<0.01$). *S. fuscicollis* mostly used vertically orientated substrates (55.7%) whereas the *S. labiatus* most often used obliquely (44.1%) and horizontally (37%) orientated substrates. Figure 2.D shows that there was a major but non-significant difference in the proportion of usage of different sized substrates ($X^2 = 5.52$, df=2). *S. labiatus* used small (44.1%), large (29.8%) and medium (26.1%) sized substrates in that order, while *S. fuscicollis* used large (45.7%), small (38.6%) and medium (15.7%) sized substrates respectively. Basically *S. fuscicollis* used medium (i.e. 5-10cm) sized substrates less often and large sized substrates more often. On the other hand *S. labiatus* used small and medium substrates more often.

Saguinus labiatus, N = 111



Saguinus fuscicollis, N = 70

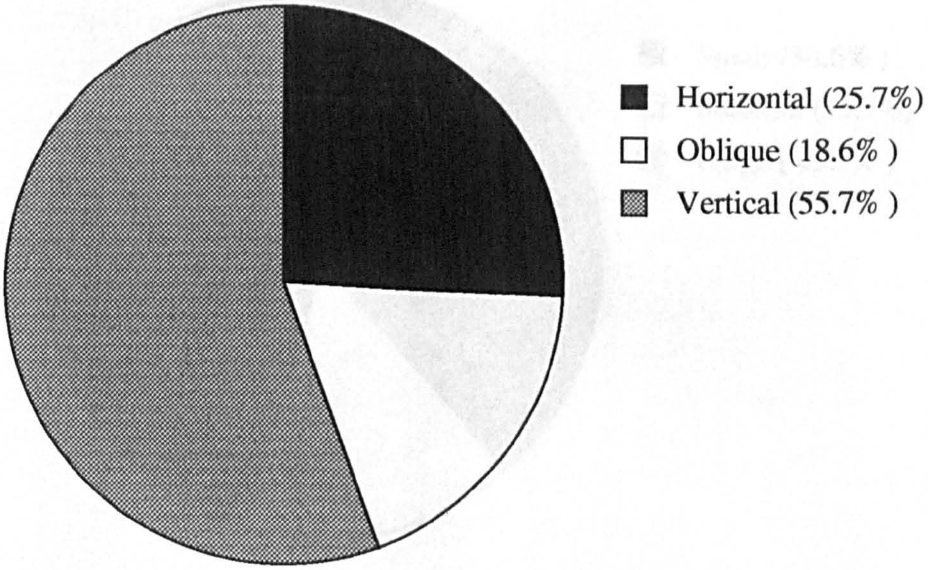
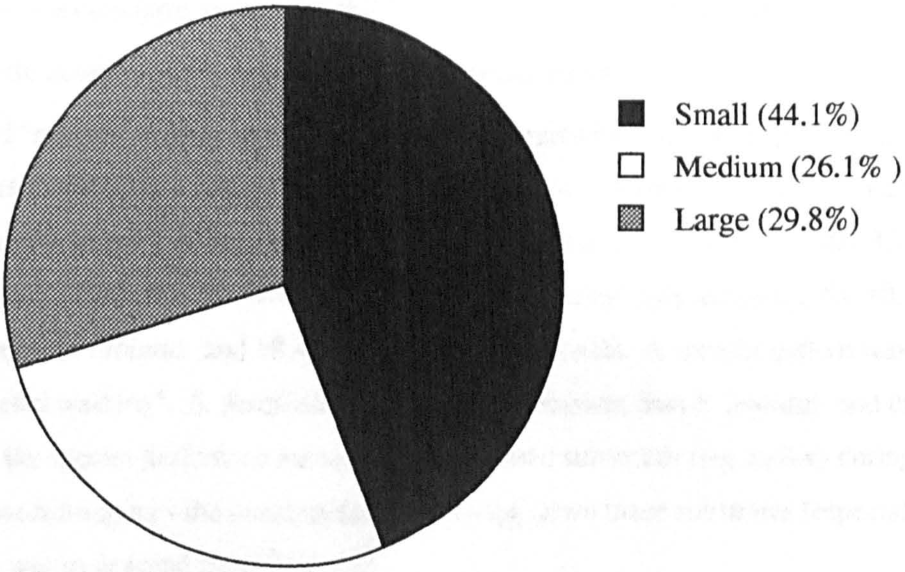
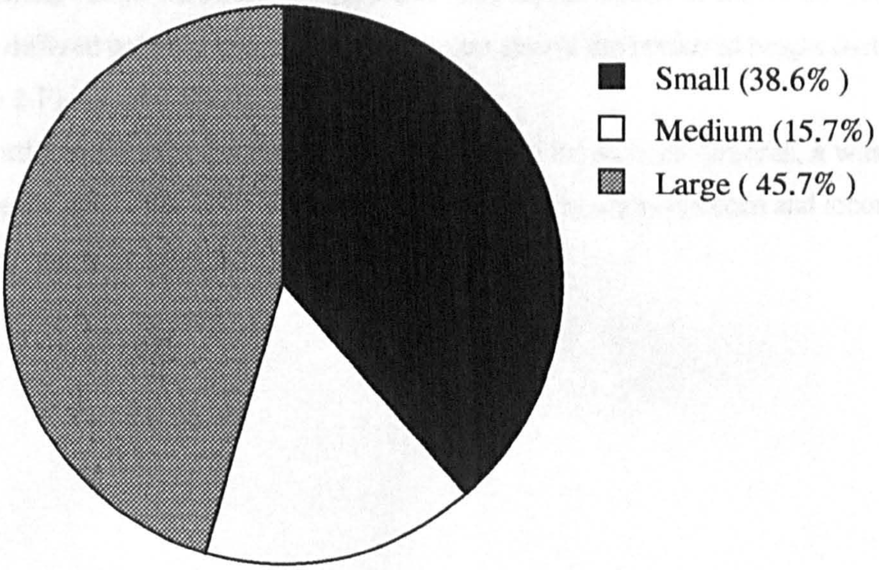


Figure 2.C : Orientation of substrate used by tamarins. Orientations were as follows ; Horizontal 0-15*, Oblique 16-74* and Vertical 75-90 * (difference was significant, Chi-Square = 26.95, df =2, p<0.01).



Saguinus labiatus, N = 111



Saguinus fuscicollis, N = 70

Figure 2.D : Size of substrate used by tamarins. Sizes were as follows : Small 0-5 cm ; Medium 5-10 cm ; Large 10 cm+ (Chi-Square = 5.52, non significant)

2.8 Locomotory differences between the species.

2.8.1 Categories of locomotion.

Due to the lack of data for other activities it was decided that only locomotion had enough sample points to justify further investigation. Initially the 2 species were compared in terms of the categories of locomotion used (Figure 2.E). From this it was obvious that the 2 species differed significantly in terms of the style of locomotion preferred ($X^2 = 29.2$. df=5, $p<0.01$). While "leap" and "ascend" accounted for a roughly similar percentage for both species, there were differences in the other 4 categories. A large difference was demonstrated in the "vertical cling and leap" category where it occurred for 28.6% of the time in *S. fuscicollis* and only 3.2% of the time in *S. labiatus* (Table 2.L). In terms of "quadrupedal running" this accounted for 40.3% of time locomoting in *S. labiatus* and 18.4% of time in *S. fuscicollis.* A similar pattern was found for "quadrupedal walking". *S. fuscicollis* descended more often than *S. labiatus* and this is probably related to the species preference for vertically orientated substrates (see earlier) during locomotion and for insect foraging - the usual method of moving down these substrates (especially when they are large) was to descend head-first.

For height used during locomotion it was obvious that there was a significant difference between the 2 species (Kolmorogov-Smirnov $D_{m,n} = 0.479$, $m = 62$, $n=49$, $p<0.001$), and with the significant difference between the locomotory styles described above, this means that the species differed not only in locomotory style but also in the preferred height during locomotion (Figure 2.F).

In order to examine the factors most responsible for these differences, it was necessary to examine the most commonly encountered pairings of height preference and locomotory style. This is shown below in Table 2.L.

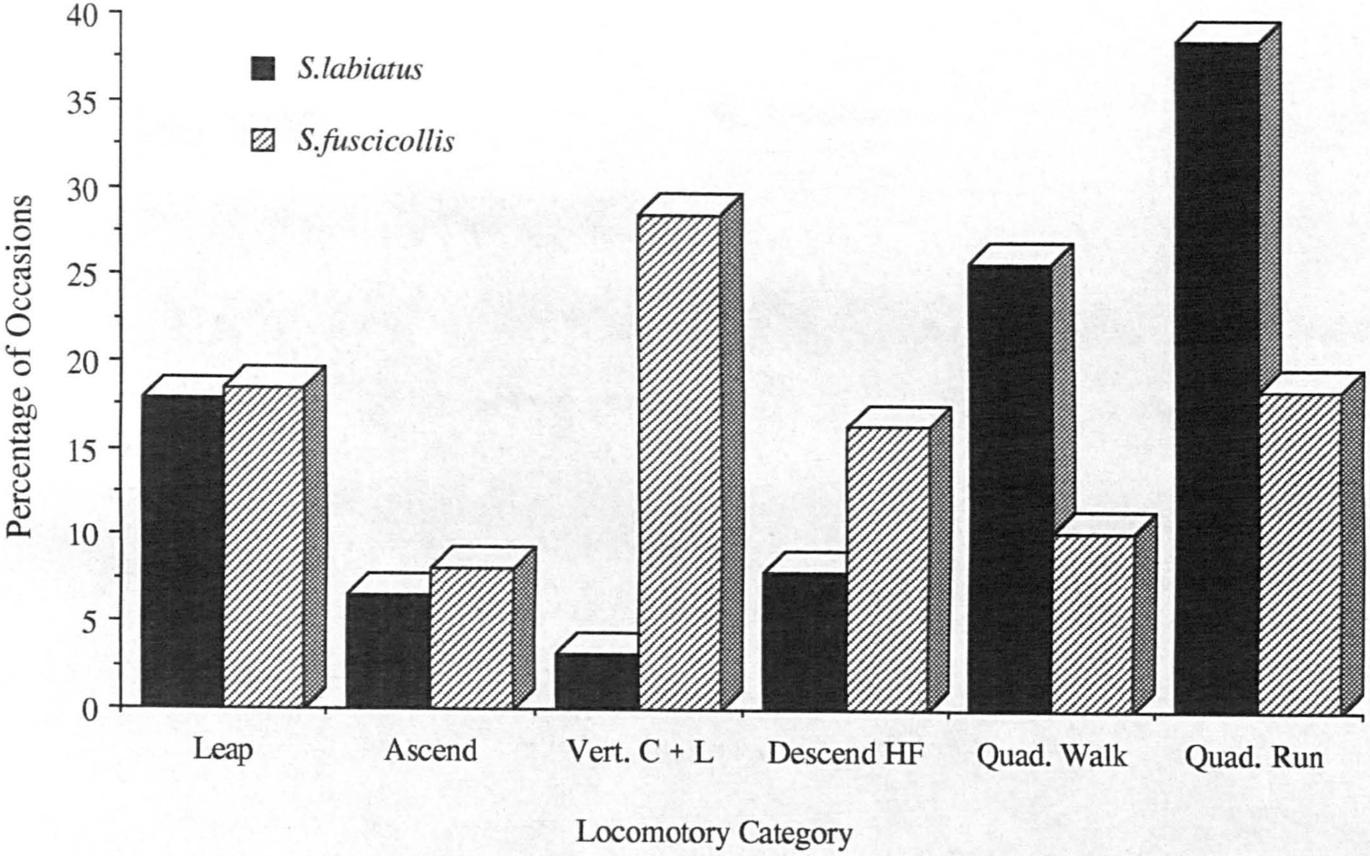


Figure 2.E : Categories of locomotion used by each species (For S.labiatus N= 62; For S.fuscicollis N= 49 : Chi-Square = 29.2, df = 5, p< 0.01).

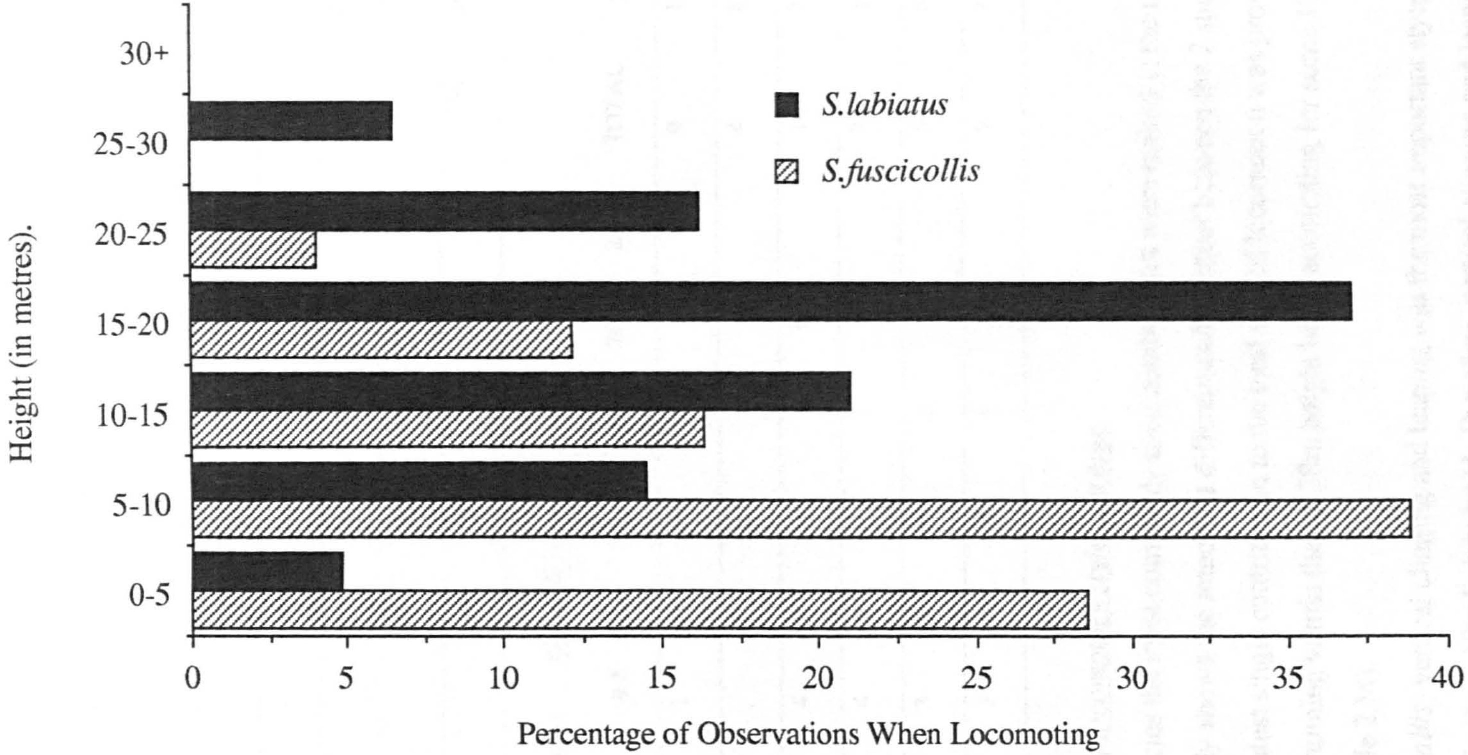


Figure 2.F : Height used while travelling by 2 species of tamarin (For S.labiatus N= 62, mean 15.7 ; For S.fuscicollis N= 49, mean 8.7m ; Kolmogorov-Smirnov D =0.479, n=62, m=49, p < 0.001)

Table 2.L : Distribution of locomotory styles over heights, by Bolivian tamarins.

Saguinus labiatus (*N = 62*)

	0-5	5-10	10-15	15-20	20-25	25-30	TOTAL	%
LEAP		2	2	5	2		11	17.7
ASCEND			3	2			5	8.1
VERTICAL C+L	1	1					2	3.2
DESCEND H.F	1		2	1		1	5	8.1
QUAD. WALK		2	3	5	2	2	14	22.6
QUAD. RUN.		2	5	11	6	1	25	40.3

Saguinus fuscicollis (*N = 49*)

	0-5	5-10	10-15	15-20	20-25	25-30	TOTAL	%
LEAP	1	2	3	3			9	18.4
ASCEND		3	1				4	8.2
VERTICAL C+L	4	7	2		1		14	28.6
DESCEND H.F	4	3		1			8	16.3
QUAD. WALK	3	1		1			5	8.1
QUAD. RUN.	3	2	2	1	1		9	18.4

2.8.2 Height and locomotory style pairings.

For each species the most commonly used combination were ranked 1; the next most common 2 etc. This clearly shows the important differences that occur between the 2 species. For *S. labiatus* the greatest single contribution to the total sum of locomotion was provided by the pairing of Quadrupedal running within the 15-20m height band, accounting for some 17.7% of total locomotion (Table 2.M).

For *S. fuscicollis* vertical clinging and leaping was the most important style and this occurred most commonly in the 5-10m height band. Therefore, vertical clinging and leaping and quadrupedal running can be described as the most important styles of locomotion for the two species ; indeed combining the scores of the top 2 ranked pairings, it is clear that they account for approximately 25% of all locomotion for both species. Coupling this with the mean height used during locomotion (see Table 2.L), shows that these measures had a large degree of influence upon the means ; the *S. labiatus* mean travel height was 15.7m, with quadrupedal running being most commonly found at the 15-25m height category, while for *S. fuscicollis*, the mean travel height was 8.7m and the most commonly used method was vertical clinging and leaping, in the region 0-10m. With this in mind, it was decided to examine the substrates used to locomote upon, paying particular reference to the average height used and to the height range used in the most common pairings.

Table 2.M : Highest ranked pairings of locomotory style and height preference for the 2 species of tamarin.

Saguinus labiatus

Rank	Locomotory Style	Height	No. of Observations	%
1.	Quadrupedal Running	15-20m	11	17.7
2.	Quadrupedal Running	20-25m	6	9.7
3. =	Quadrupedal Running	10-15m	5	8.1
3. =	Quadrupedal Walking	15-20m	5	8.1
3. =	Leaping	15-20m	5	8.1

Saguinus fuscicollis

Rank	Locomotory Style	Height	No. of Observations	%
1.	Vertical Cling + Leaping	5-10m	7	17.7
2. =	Vertical Cling + Leaping	0-5m	4	8.2
2. =	Descending Head First	0-5m	4	8.2

Top 2 ranking of pairs combined : *S. labiatus* Q-run 15-25m = 27.4%
: *S. fuscicollis* V. C+L 0-10m = 22.5%

2.9 Substrate use during locomotion.

2.9.1 Size of substrate.

For the overall substrate use by the 2 species there was no significant difference. Both species clearly preferred to use small and large sized substrates more than medium sized ones. Comparing the pattern of substrate size to height some patterns emerged. Figure 2.G [I] shows that for *S. labiatus* small sized substrates are avoided at low (0-5m) and high (25m+) heights, but are used for a large amount of time in the intermediate height categories. Additionally, medium sized substrates were used in all height categories between 0-30m. Large substrates were also used in all height categories and were used as often as small sized substrates. With a mean travel height of 15.7m it is clear that small (<5cm) sized substrates were the most commonly used substrates in this height category. Looking at the 15-25m height band, small sized substrates accounted for the largest percentage (44.5% : 16/36 observations). This height category encompassed the lower and middle canopy area of the forest (see earlier section) and coincided with the observation of locomotion predominantly consisting of quadrupedal progression in this species.

Figure 2.G (I) Size of substrate used during locomotion by S.labiatus

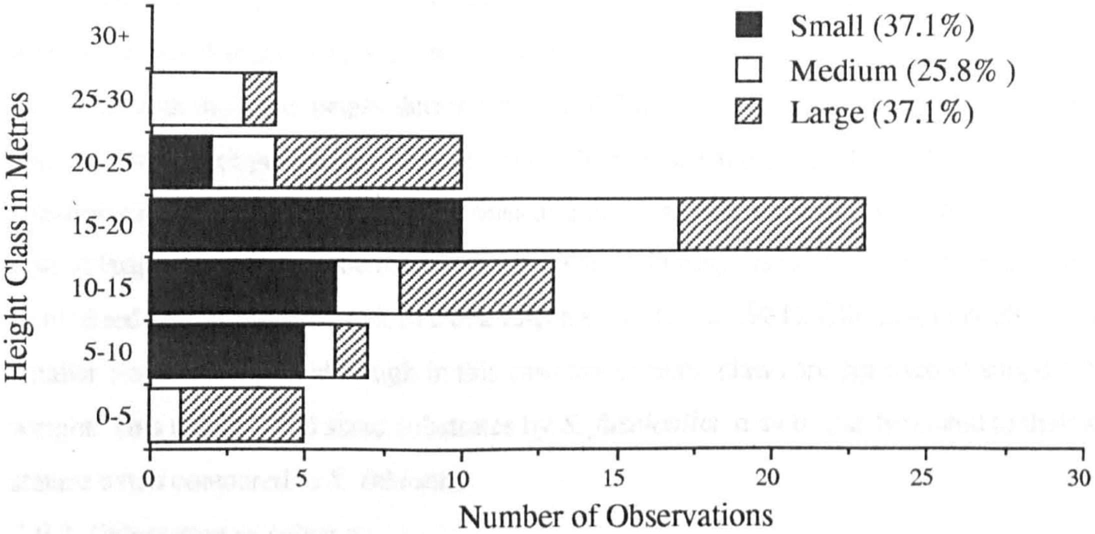


Figure 2.G (II) Size of substrate used during locomotion by S.fuscicollis

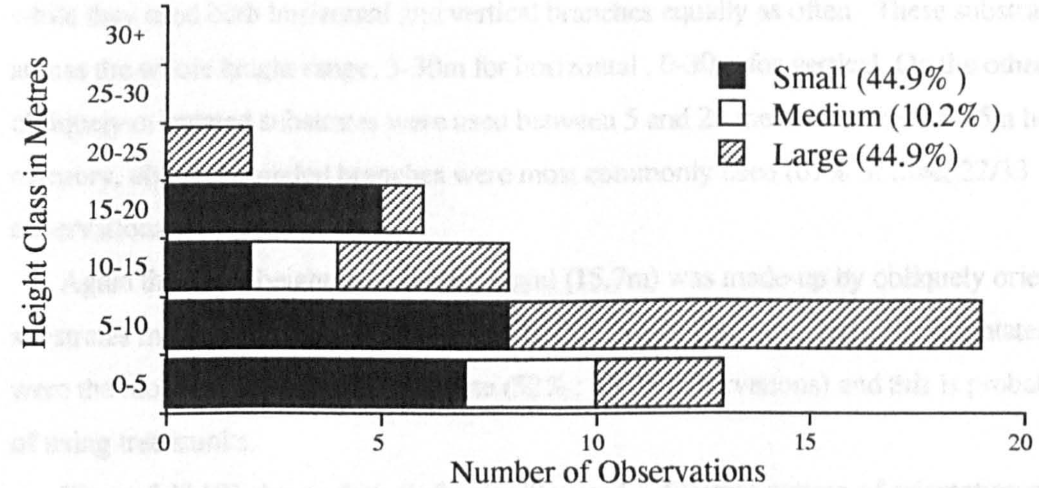


Figure 2.G : Size of substrate used by Bolivian tamarins, over height categories.(overall size of substrate used ; $X^2 = 4.34$, df = 2, non-significant).

In *S. fuscicollis* medium sized substrates were not used very often (Figure 2.G[II]). Small sized substrates were used more than in *S. labiatus*, as were large sized ones. Medium sized substrates were used in the 0-20m height band as were small sized ones. Large sized substrates were used in all height categories, but were most commonly used in the 5-10m height band - which coincides with the mean height during travel of 8.7m. In this height category large substrates were used for the largest percentage of time (39% : 7/18 observations). In the 0-10m height band, small substrates were used as often as large ones and this was very different from the use of *S. labiatus*. Use of large substrates can be related to the vertical clinging and leaping that often occurs between large sized tree trunks (= trunk to trunk leaping; cf. Izawa, 1981). Clinging may also occur on smaller sized substrates, although in this case the animals' claws are <u>not</u> used to support their weight. This use of small sized substrates by *S. fuscicollis* may be partly related to their smaller stature when compared to *S. labiatus*.

2.9.2 Orientation of substrate.

Figure 2.H [I] shows that the orientation of substrates used by the two species was significantly different ($X^2 = 15.76$, df=2, $p < 0.01$), in terms of overall use of differently orientated substrates. *S. labiatus* locomoted predominantly on obliquely orientated substrates, while they used both horizontal and vertical branches equally as often. These substrates were used across the whole height range; 5-30m for horizontal, 0-30m for vertical. On the other hand, obliquely orientated substrates were used between 5 and 25 metres. in the 15-25m height category, obliquely angled branches were most commonly used (67% of time; 22/33 observations).

Again the mean height used during travel (15.7m) was made-up by obliquely orientated substrates most often. Interestingly, in the 0-15m height category, vertically orientated substrates were the most commonly used substrate (52% : 13/25 observations) and this is probably indicative of using tree trunks.

Figure 2.H [II] shows that *S. fuscicollis* used a different pattern of orientation of substrates. Vertically orientated substrates were the overall preferred substrate for travel. In the height category 0-15m, *S. fuscicollis* used vertically orientated substrates for much of the time (61% : 25/41 observations < 15m). With a mean height during travel of 8.7m, it is no surprise that vertically orientated substrates were used some 84% of the time in the 5-10m band.

Horizontally and obliquely orientated substrates were not used very often, although they were used in most of the height range. In the 20-25m height band they were used more often than vertically orientated substrates, a pattern similar to that in *S. labiatus*.

Figure 2.H (I) Orientation of substrate used by S.labiatus during locomotion

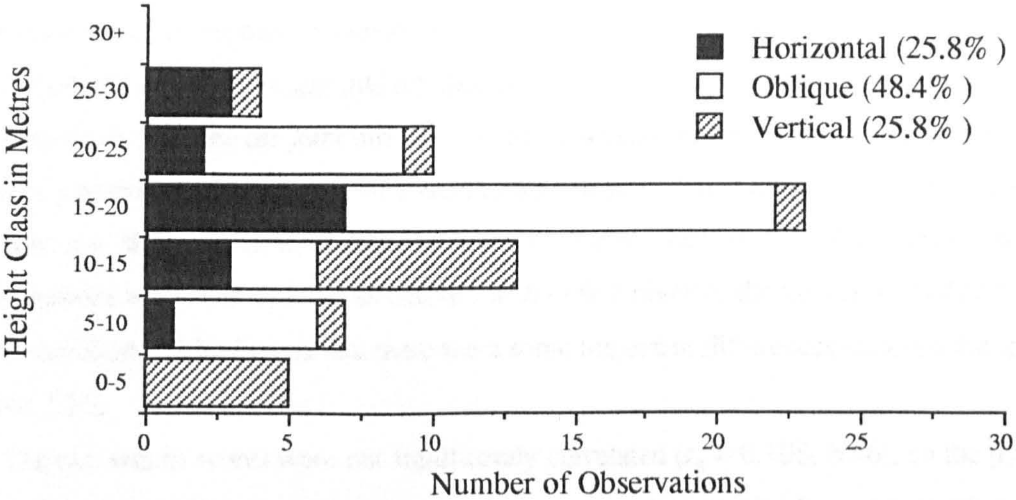


Figure 2.H (II) Orientation of substrate used by S.fuscicollis during locomotion

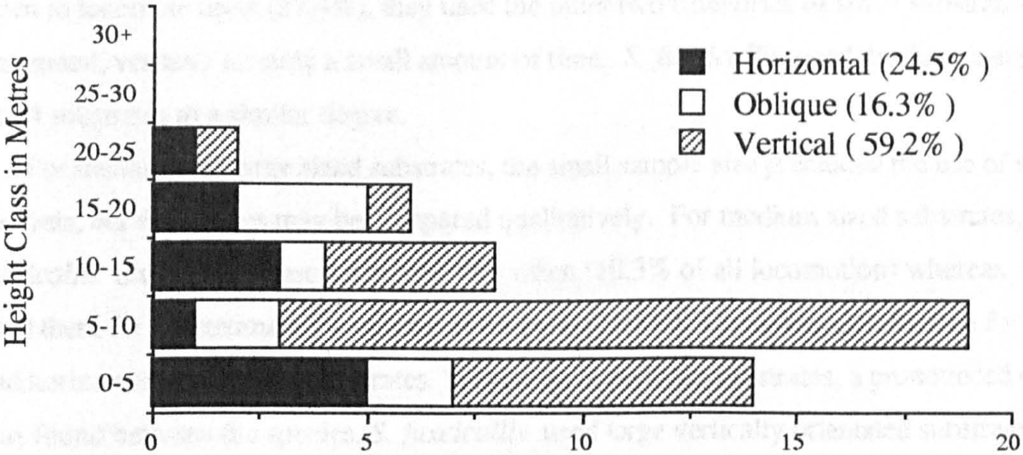


Figure 2.H : Orientation of substrate used by Bolivian tamarins, over height categories (overall orientation used during locomotion ; $X^2 = 15.76$, df=2, $p < 0.01$).

This suggests that the use may be affected by the availability of these substrates, where this higher height class contains the predominantly obliquely and horizontally orientated crowns and lower-middle canopy of trees. The lower (<10m) height category contains many of the vertically orientated trunks of the high crowned tree species typical of the Neotropics.

2.9.3 *Pairings of substrate size and orientation.*

In order to examine the joint influence of substrate size and orientation upon locomotion, it was necessary to examine the number of observations that were found to occur in each subcategory of pairings (e.g. large ; vertical, oblique, horizontal. : Small ; vertical etc.). The scores in the nine subcategories were rank ordered as before, with rank 1 given to the largest right down to rank 9 for the smallest. This showed that there were some important differences between the species (Table 2.N).

The two sets of scores were not significantly correlated ($r_s = 0.108$, N=6), so the pattern of substrate use differed between the species. As the size and orientation have previously been examined separately, the most important area to be examined was the interaction between these two factors. Overall there was a significant difference in the pattern of small sized substrates ($X^2 = 6.11$, df = 2, $p<0.05$). Although *S. labiatus* used small / obliquely orientated substrates most often to locomote upon (27.4%), they used the other two categories of small substrates (i.e. horizontal, vertical) for only a small amount of time. *S. fuscicollis* used the three categories of small substrates to a similar degree.

For medium and large sized substrates, the small sample size precluded the use of statistical analysis, but the species may be compared qualitatively. For medium sized substrates, *S. fuscicollis* did not use these substrates very often (10.3% of all locomotion) whereas *S. labiatus* used them for approximately a quarter of the time (25.8%). There was a preference for obliquely and horizontally orientated substrates. Within the large sized substrates, a pronounced difference was found between the species. *S. fuscicollis* used large vertically orientated substrates to locomote upon during 38.8% of observations, whereas *S. labiatus* used similarly sized substrates for only 17.7% of the time. Large horizontally inclined substrates were infrequently used by both species and large sized obliquely orientated substrates were used only by *S. labiatus.*

Table 2.N : Pairings of substrate size and locomotion, for *S. labiatus* and *S. fuscicollis* (r_s = 0.108, N=6, non-significant).

	S. labiatus			*S. fuscicollis*		
I : Small	N	%	Rank	N	%	Rank
Horizontal	4	6.5	7	8	16.3	2=
Oblique	17	27.4	1	8	16.3	2=
Vertical	2	3.2	9	6	12.2	4
	X^2 = 6.11, df =2, p< 0.05					
II : Medium	N	%	Rank	N	%	Rank
Horizontal	7	11.3	3=	1	2.3	7
Oblique	6	9.7	5	0	-	8=
Vertical	3	4.8	8	4	8.2	5
III : Large	N	%	Rank	N	%	Rank
Horizontal	5	8.1	6	3	6.1	6
Oblique	7	11.3	3=	0	-	8=
Vertical	11	17.7	2	19	38.8	1

It was decided to examine the most commonly used pairings in detail, so that the reasons behind these differences could be understood (Table 2.O). The use of large vertically orientated substrates during locomotion by *S. fuscicollis*, was linked intrinsically with their use of vertical clinging and leaping to locomote. This corresponded with their use of large, vertically orientated trunks to move upon and *S. fuscicollis* used their claws to cling to the large trunks. The mean height used (8.55m) corresponds to an area of the forest that contains many large sized trunks. The use of ascending and descending and leaping is linked to their movements up and down in the vertical plane, while the vertical clinging and leaping strategy is their chosen method for locomoting, mainly within the 0-10m height band.

For *S. labiatus* their use of small obliquely orientated substrates showed the importance of quadrupedal progression (both running and walking) and leaping for these monkeys. The mean height used (14.6m) corresponds to the lower to middle canopy area and these monkeys walked and ran within the crowns and between the adjacent trees.

Table 2.0 : Locomotory style and height used to travel upon most commonly used substrate pairings.

A: *Saguinus labiatus*		**Small / Oblique**	
Style		Height	
Leap	7	0-5m	-
Ascend	-	5-10m	4
Vertical C + Leap	-	10-15m	3
Descend	-	15-20m	9
Quadrupedal Walk	3	20-25m	1
Quadrupedal Run	7	25-30m	-
		25m+	-
	N = 17		**Mean = 14.56m***

B: *Saguinus fuscicollis*		**Large / Vertical**	
Style		Height	
Leap	1	0-5m	4
Ascend	3	5-10m	10
Vertical C + Leap	12	10-15m	3
Descend	3	15-20m	1
Quadrupedal Walk	-	20-25m	1
Quadrupedal Run	-	25-30m	-
		25m+	-
	N = 19		**Mean = 8.55m***

* using midpoints of height categories.

The two species differed not only in average height of locomotion but also in terms of the posture and substrate types used to locomote within the preferred height of forest.

2.10 Discussion.

In the past the Pando region of northern Bolivia has been categorised as having one of the broadest spectra of primate species in South America (e.g. Izawa 1979; Pook & Pook, 1981; Cameron & Buchanan-Smith, in press). In terms of primate species diversity and distribution, the main study site was found to be almost as rich as the other intensively studied areas of Bolivia (see Freese *et al.,* 1982 ; Pook & Pook,1982; Izawa & Bejarano, 1981; Buchanan-Smith,1989). Nine distinct species of primate were found at Bella Flor, and there were in total ten different species encountered. This corresponds with the figure of the at least 14 reported separate species, believed to occur in Bolivia (Garcia & Cases, 1989; Mittermeier *et al.,* 1989 ; Cameron & Buchanan-Smith, in press).

The cebids encountered in the present study were essentially identical to those found in studies at other parts of the Pando (e.g. Izawa & Bejarano, 1981). The larger primates (i.e *Callicebus, Cebus, Alouatta, Pithecia*) were not observed very frequently, and were extremely nervous of humans. Cebids are usually found much more infrequently than callitrichids (e.g. Rylands & Keuroghlian,1988) and *Pithecia* in particular, are always considered to be rare (Buchanan *et al.*, 1981). As the study sites were always populated by humans, the most probable reason for scarcity of sightings being that they were extensively hunted for food; which unfortunately, is sadly all too commonplace throughout South America (see Mittermeier *et al.*, 1989). Only the *Saguinus* species were encountered with any large frequency, once again a commonly found pattern within this region (Cameron *et al.*, 1988; Buchanan-Smith, 1989; Kolhaas, 1991).

The occurrence of both *S. labiatus* and *Pithecia irrorata* only as far as Rio Tahuamanu has been suggested previously (Izawa & Bejarano,1981) and was confirmed in this study. In all excursions over the river, no-one that was questioned (using descriptions and photographs) reported seeing either species, nor did I find any trace in terms of sightings, vocalisations, nor pelts of dead animals. Although this study was in no way exhaustive, coupling it with other studies on the south bank of the Rio Tahuamanu (e.g. Buchanan-Smith, 1989; Izawa & Bejarano,1981; Freese *et al.*,1982) provides support that the distribution of *S. labiatus* ends there. Recently, Encarnacion (1990) reported that *S. labiatus* was found only on the left bank of the Tahuamanu in Peru. Prior to this, Hershkovitz (1977) indicated that the width and force of the Rio Madre de Dios may block the advancement of the *Saguinus mystax* (white-lipped tamarin) group. While *S. imperator* can be found south of the Tahuamanu (see Izawa & Bejarano, 1981 for a report of *S. imperator* at Rio Muyumanu, between Rios Tahuamanu and Manuripi) the available evidence suggests that in northern Bolivia *S. labiatus* is found only as far south as Rio Tahuamanu and not as far as Madre de Dios, as Hershkovitz (1977) suggested. In a recent review of distribution, Rylands *et al.*, (1993: 62) agreed with this position and state that *S. labiatus* are "probably limited to the Rio Tahuamanu".

S. fuscicollis were observed to occur on both sides of Rio Tahuamanu and they are probably found at least as far as Madre de Dios (Hershkovitz,1977; Izawa & Bejarano,1981; Rylands, *et al.*, 1993). The areas between Rios Tahuamanu and Manuripi and Madre de Dios (see Figure 2.A) are relatively unexplored, and may contain previously unknown species and/or sub-species. As rivers are usually constraining factors on species' dispersal (Ayres & Clutton-Brock,1992), it remains an interesting proposal to explore the fauna of these areas.

The occurrence of *Callimico goeldii* in Bella Flor provided an additional point of location for this species, again more easterly than other previous studies. As it was observed in three or four close localities to the Bella Flor area (<5km), this supports the view that Bolivia may contain one of the highest densities of this species in South America (Cameron et al., 1988; Pook & Pook, 1981). It was clear that this species was very rarely observed and was extremely nervous when encountered. On the surface it appears that *C. goeldii* may have a non-continuous and 'patchy' distribution, being inexplicably absent and present in apparently similar areas (Christen & Geissmann, 1994; Izawa, 1979; Masataka, 1981a,b). This could partially explain the lack of encounters, as could their large home range (50-60 ha, Pook & Pook,1981) and low population density (between 1.5 Inds. / Km^2 ; Pook & Pook,1981 and 8 Inds. / Km^2 ; Cameron et al., 1988). Overall it still remains a mystery as to what constraints affect the distribution of this primate.

2.10.1 Mixed-species groups.

Mixed-species groups of tamarins have been found for all three members of the *Saguinus mystax* group (Hershkovitz,1977) and estimates of the percentage of sightings usually ranged from between 50-100% of encounters (see Glander *et al.*,1984; Heymann, 1990b; Norconk, 1990b; Freese *et al.*, 1982; Peres,1991,1992a; also Chapter 1). The encounters with mixed groups in the present study (83% for *S. fuscicollis* ; 86% for *S. labiatus*) are of a similar occurrence to those found previously. While there is always the possibility of monospecific groups occupying territories (see Terborgh,1983 for an example), the study area appeared to be occupied mainly by mixed-species groups. This was generally believed to be the case in areas of previous studies of *Saguinus* associations (e.g. Heymann,1990b; Norconk,1990b; Buchanan-Smith,1989). Also, observations of monospecific groups does not necessitate that these groups are not forming mixed-species groups. Indeed, monospecific groups of both species can additionally be explained by the finding that the associating species do not spend all their time in association. For example, in *S. labiatus* and *S. fuscicollis* daily association levels could average as low as 43-57% of time (Pook & Pook, 1982), or as high as 84% (Buchanan-Smith,1989), dependent upon habitat seasonality and /or observation techniques. Therefore at any point in time some associating groups will not be in association. Thus when encountering a monospecific group it is feasible that it may be part of a mixed group that is not in association at that time.

The frequency of sightings of mixed-species groups in the present study (86% for *S. labiatus*) was similar to the average frequency of association (84%) in Buchanan-Smith's (1990a) main study group of *S. labiatus* and *S. fuscicollis*, and can be favourably compared to that of other mixed *Saguinus* groups (Table 2.P). However, the result of Kolhaas's (1991) study stands out as being much lower than the other studies. As this study was conducted near to Villa Busch, a small settlement between Cobija and Porvenir (see Figure 2.A), the population of primates was probably subject to a more intense hunting pressure than the other more distant study sites, probably contributing to generally lower densities.

Table 2.P : Percentage of association in various *Saguinus* mixed-species groups.

Association	%	Type	Reference.
S. fuscicollis & S. mystax	58	2	Castro & Soini, 1978.
	53	2	Glander *et al.*, 1984.
	100	2	Ramirez, 1984.
	62	1	Heymann, 1990b.
	82	2	Heymann, 1990b.
	98	1	Peres, 1992a.
	74	1	Garber, 1988a.
S. fuscicollis & S.imperator	100	2	Freese *et al.*, 1978.
S. fuscicollis & S. labiatus	50	1	Pook & Pook, 1982.
	68	2	Pook & Pook, 1982.
	84	1	Buchanan-Smith, 1989.
	39	2	Kolhaas, 1991.
	75	**2**	**This Study.**

Notes

1) Percentage association of main group, i.e. percentage of observations centred around one group.

2) Percentage of all groups encountered that were found in mixed species groups.

Observations of Pithecia irrorata* feeding high in trees with *Saguinus* species have been noted previously (Buchanan-Smith,1989, 1990b; Izawa & Bejarano,1981: * named as *P.hirusita,* but may (probably) be *P.irrorata*- Buchanan-Smith,1990a,b). These, as in the present study, appear to be limited to "chance encounters" between species sharing a common resource and do not involve the coordinated and non-random grouping that characterises *Saguinus-Saguinus* associations (e.g. Norconk, 1990b).

Pook & Pook (1982) describe a three way association between *S. labiatus, S. fuscicollis* and *Callimico goeldii,* where all three associate in the same cohesive manner that the tamarins do. The *Callimico* appeared to have a larger range than the *Saguinus* species, and this may allow them to associate with more than one pairing of *Saguinus* groups. In the present study the extreme shyness and the infrequent contact with *Callimico,* meant that no "association" could be determined that varied from a random aggregation. Nor was there any obvious sign of integrated travel with the tamarins, as described by the Pooks.

2.10.2 Group size of tamarins.

While discussion on callitrichid mating system, group composition and stability continues (see Price,1991), these issues were not quantitatively considered in the present study. The only relevant finding was that only one set of offspring was observed in any single group. The main data collection on groups involved estimates of group size and these are discussed below.

Table 2.Q shows that in terms of mean group size for each species the results found were within the range of means shown in other studies. The mean group size of *S. labiatus* (6.1) was very similar to that of Buchanan-Smith's (1990a) study and was at the upper-middle end of the range of means. The results for *S. fuscicollis* were again broadly similar to the published means. The present mean group size for *S. fuscicollis* (5.7) was again similar, and lower than, the mean in Buchanan-Smith's (1990a) study, but was well within the 'usual' range of means (see Table 2.Q).

Table 2.Q : Group size of *Saguinus labiatus* and *Saguinus fuscicollis.*

I : *S. labiatus* in Mixed-Species Groups

N	Range	Mean	Reference.
10	2-6	4.2	Yoneda, 1981.
2	4-5	4.5	Pook & Pook, 1982.
7	1-13	5.7	Freese *et al.*, 1982.
27	3-8	6.6	Castro (cited in Sussman & Kinzey, 1984).
6	(2-6?)	4.3	Castro *et al*, 1981(cited in Snowdon & Soini,1988).
12	5-10	6.3	Buchanan-Smith, 1990a.
47	1-8	2.7	Kolhaas, 1991.
15	**4-11**	**6.1**	**This Study.**
		5.02	*Overall Mean*

II : *S. fuscicollis* in Mixed-Species Groups

N	Range	Mean	Reference.
13	2-7	4.7	Yoneda, 1981.
2	5-9	7	Pook & Pook, 1982.
16	2-9	5.0	Freese *et al.*, 1982.
21	1-7	4.1	Castro (cited in Sussman & Kinzey, 1984).
375	1-17	5.7	Castro (cited in Snowdon & Soini, 1988).
15	2-9	6.5	Buchanan-Smith, 1990a.
59	1-6	3.7	Kolhaas, 1991.
7	2-10	?	Terborgh & Goldizen, 1985.
?	?	5	Terborgh, 1983.
25	2-9 (+ 1x15-26)	2-6 (mode)	Castro & Soini, 1978.
11	3-14	5.4	Ramirez, 1984.

N	Range	Mean	Reference.
11	4-12	7.1	Glander *et al.*, 1984.
16	3-9	5.6	Castro *et al*.,1981 (cited in Snowdon & Soini,1988).
?	?	6.4	Peres, 1991(with *S.imperator*)
?	?	6	Cameron *et al.*, 1988.
1	7-9	8	Garber, 1988a.
1	6	6	Heymann, 1990b.
6	?	5.5 (range 3.7-5.6)	Peres, 1991(with *S. mystax*)
9	4-10	5.5	Ramirez, 1984.
2	4-11	?	Norconk, 1990b.
?	5-10	?	Hernandez-Camancho & Cooper, 1976 (with *S.nigricollis*).
11	**3-8**	**5.7**	**This Study.**
		5.72	*Overall Mean*

III :*S. fuscicollis* in Single Species Groups

N	Range	Mean	Reference.
?	2-10	6 (mode)	Soini, 1987.
20	2-7	4.3	Moynihan, 1976.
62	3-12	5.8	Soini, 1983 (cited in Snowdon & Soini,1988).
?	5-40+	10	Izawa, 1976.
1	6-10	8	Soini, 1987b.
4+	4-15	?	Neville *et al.*, 1976.
?	?	6	Freese *et al.*, 1982.
		6.68	*Overall Mean*

Previous studies of group size in mixed *S. labiatus* and *S. fuscicollis* troops usually found that the mean group size of *S. fuscicollis* was greater. For example, Yoneda,1981; Pook & Pook,1982; Buchanan-Smith,1990a and Kolhaas,1991, all found a higher mean group size for *S. fuscicollis.* In the present study, as was the case for both Castro (cited in Sussman & Kinzey,1984) and Freese *et al.*, (1982), it was found that the mean group size of *S. labiatus* was greater.

The present study's maximum observed group size (11) was also larger for *S. labiatus* than for *S. fuscicollis.* This pattern was the same in four of the previous studies (Castro, cited in Sussman & Kinzey,1984; Freese *et al.*, 1982; Buchanan-Smith,1990a; Kolhaas, 1991) and was the reverse of two other studies (Yoneda,1981; Pook & Pook,1982), both of which were carried out in areas where trapping was being conducted (Galindo-Franco, pers. comm.). The largest overall group size (13) of tamarins in these mixed troops was found for *S. labiatus*, and in this type of association *S. fuscicollis* appear never to have been encountered in groups of 10 or more individuals. So for *S. labiatus* there is a suggestion that maximum group size is larger, although the position of average group size and population density is far from clear.

Finally, as the *S. labiatus* were much more nervous of humans than the *S. fuscicollis*, it is fair to assume that the observed differences were not an artifact of differential observability in numbers between the species. Of additional importance, may be the fact that the location of the present study ; it was conducted some 100 kilometres east of all previous studies in Pando. The differences may be therefore related to habitat, and this should be investigated in future studies.

2.10.3 Birth of infants.

Births were found to occur at different times of the year, at least for *S. fuscicollis*, but some tentative evidence (due to the paucity of data) suggests that there may be more groups giving birth in the period October -November than in May-September. This pattern was also found in a similar previous study (Buchanan-Smith,1989).

In captive tamarins, there is a potential for tamarins to give birth every six months (e.g. Wolfe *et al.*, 1975 ; Snowdon & Soini,1988), whilst in the wild there is usually only a single litter per year (Neyman,1980; Terborgh,1983). This is thought to be influenced by seasonality of resources and high costs of lactation in tamarins (Goldizen, & Terborgh,1989). In non-Amazonian tamarin species (e.g. *S.oedipus*, *S.geoffroyi*) births may occur throughout the year, but relatively few are found outside the birth peak of April to June (Moynihan, 1970; Dawson & Dukelow,1976). For Amazonian tamarin species, the peak occurs from around October - February (e.g. Izawa,1978; Pook & Pook, 1982; Terborgh,1983; Soini, 1987). In both cases, these yearly peaks are thought to coincide with the time of greatest fruit availability (i.e. early rainy season) and these allow the animals to maximise reproductive output. The tendency for births to occur around the peak level of food availability has long been postulated (Charles-Dominique, 1977 ; van Schaik & van Noordwijk, 1985) and has been quantitatively shown in *S. fuscicollis* (Goldizen *et al.*, 1988). This pattern is probably also found in the present study.

2.10.4 Sleeping tree.

Only one sleeping site was discovered during the study, and this was only for *S. labiatus*. It was a hole at the top of a tree, where part of the trunk had been broken off. The use of holes for tamarins to sleep in has been noted in previous studies for *Leontopithecus rosalia* (Coimbra-Filho,1978), *S. geoffroyi* (Moynihan, 1976) and occasionally in *S. fuscicollis* (Terborgh,1983; Yoneda 1984a). More commonly, tamarins have been reported to roost in tree-forks and vine-tangles (Buchanan-Smith,1991a; Dawson,1979; Peres,1991; Soini, cited in Snowdon & Soini,1988).

2.10.5 The use of plant resources.

Some 16 distinctive plant food species were recorded for the two species, and 10 of them were definitely shared. The two main families of plants used were *Leguminoseae* and most commonly *Moraceae*. These plant families have been previously shown to be important components of tamarin diets (e.g. Garber,1993a,b; Neyman,1980; Terborgh, 1983), and those of other South American primates (e.g *Callithrix* : Rylands,1981; *Ateles* : van Roosmalen & Klein,1988; *Brachyteles* : Nishimura *et al.*, 1988; *Chiropotes* ; Kinzey & Norconk, 1990). Indeed, in common with several other tamarin studies, *Moraceae* was the singularly most exploited plant family (Buchanan-Smith,1989; Soini,1987; Terborgh, 1983; Yoneda,1984a).

Five of the main types of fruit consumed in the present study (*Pourouma, Pseudolmedia, Cecropia, Inga & Brosmium*) can be compared with other field data (Table 2.R). All have been shown to be consumed by different species of tamarins, in different localities,with each species consuming at least two of the same genera as the present study. Also, all five genera were recorded in the other main study of *S. fuscicollis* and *S. labiatus* in Bolivia (Buchanan-Smith, 1989) for both species, and four of them also appeared in Yoneda's (1984a) study of *S. fuscicollis*.

Of added interest was the fact that all species consumed *Pourouma* spp., which not surprisingly Terborgh (1983) lists as a major resource relied on by tamarins, and over 80% of them also consumed *Inga* spp. and *Cecropia* spp. Garber (1993b) has recently argued that these three species are amongst a small group of plant genera that tamarins uniquely target and depend upon, and this can be linked to the fact they are only opportunistically used by other larger New World primate species (Rylands,1987). This may be because of their distribution and and varied ripening schedule, which means they are available in such small amounts as to be energetically unprofitable for larger primates to rely upon (Terborgh, 1983).

Although the use of *Brosmium* spp. was not reported for all the Amazonian tamarin species, they are consumed very frequently by many other species of primates. For example, they are consumed by *S.oedipus* ; Neyman,1980; *Callithrix h. intermedius* ; Stevenson & Rylands,1988; *Ateles* ; van Roosmalen & Klein, 1988; *Chiropotes* ; Kinzey & Norconk,1990; *Alouatta* ; Neville *et al.*, 1988; *Callicebus* ; Kinzey,1981; and *Cebus* & *Saimiri* ; Terborgh, 1983. This tall, large crowned, tree species (see Table 2.J), produces relatively large amounts of fruit which is probably consumed by all primate species where it is encountered (Rylands,1987). This may be related to these soft pulpy fruits being abundant, and easily digestible (Terborgh,1983). The use of these fruits in the present study, when compared to other studies, may be due to the selective hunting of larger primates in the study area, thus reducing potential competition and increasing availability. Or alternatively , as the plant community in Pando is poorly known, these trees may be more abundant in the study area, when compared to other sites.

Table 2.R : Some selected genera of plant species exploited by Amazonian tamarin species (As tropical rain-forests have great plant species variety, species are compared only at the level of genus here).

	Pourouma	Pseudolmedia	Cecropia	Inga	Brosmium	Ref.
S.imperator	✓			✓	✓	[1]
S. labiatus	✓	✓	✓	✓	✓	[2]
S. labiatus	✓		✓			[7]
S. mystax	✓		✓	✓		[4]
S.m.pileatus	✓	✓	✓	✓	✓	[8]
S.f.weddelli	✓	✓	✓	✓		[3]
S.f.weddelli	✓		✓	✓	✓	[1]
S.f.weddelli	✓	✓	✓	✓	✓	[2]
S.f.nigrifrons	✓		✓	✓		[4]
S.f.illigeri	✓		✓	✓	✓	[5]
S.f.avilapiresi	✓	✓	✓	✓	✓	[8]
S.nigricollis	✓	✓				[6]
S. labiatus	✓	✓	✓	✓	✓	[9]
S.f.weddelli	✓	✓	✓	✓	✓	[9]

References

[1] Terborgh,1983. [2] Buchanan-Smith,1989. [3] Yoneda,1984a. [4] Garber,1986;1988a,b.
[5] Soini,1987. [6] Izawa,1978. [7] Izawa & Yoneda,1981. [8] Peres,1991. **[9] This study.**

While *Pseudolmedia* is generally reported as food resources for Bolivian tamarins (e.g. Yoneda,1984a; Buchanan-Smith,1989), it has not been widely reported for other tamarins (see Table 2.R). Indeed, it was not used by either species in Terborgh's (1983) study, even though it was widely used by *Alouatta, Saimiri* and *Cebus.* It has been reported as being consumed by *Callithrix* (Stevenson & Rylands,1988) and *Ateles* (van Roosmalen,1985). So with its large amount of fruit and medium-large crown, *Pseudolmedia* can probably be considered to be another universally consumed plant species.

The small fruits from the *Celtis* vine are amongst the 'keystone' resources systematically relied upon by tamarins in Peru (Terborgh,1983). This means that while they are once again consumed by other larger primates (*Alouatta* : Neville *et al.*, 1988; *Ateles* : van Roosmalen & Klein,1988; *Saimiri, Cebus, Aotus & Callicebus* : Terborgh, 1983), they are not relied upon to any great degree. These fruits are also consumed by tamarins in other areas (e.g. Soini, 1987), but are strangely absent from the reports of other studies in Pando (e.g. Buchanan-Smith,1989 ; Pook & Pook, 1981,1982; Yoneda,1984a). However, these studies were invariably carried out in the end of the dry season to early rainy season, and may have simply 'missed' this resource being used.

Use of *Dialium guianense*, has not been recorded in any of the other tamarin studies reviewed, but has been found in the diets of *Alouatta* (Silva-Lopez *et al.*, 1993) and *Ateles* (van Roosmalen, 1985). It was only used as one of the many different plant types consumed in the complex diets of these primates. On the other hand, Stevenson & Rylands (1988: 153) reported that *Callithrix p. kuhli* (now regarded as *C.kuhli* ; Rylands *et al.*,1993) "fed extensively" on this resource, whereas *C.h.intermedius* did not, even though it was abundant in their range. This suggests that the availability of other resources and/or differential learning about food resources in groups and populations may affect food choice. In the present case, *D. guianense* was eaten only during the dry season. More importantly the feeding tree was found located adjacent to an area where a three-way intergroup encounter was observed, and the 'winning' (i.e. remaining) group ate the fruits soon after the encounter ended. As Garber (1988a,1993b) has reported that many of these encounters are conducted close to important resources, and as I noted no other main food trees within 50m, it is probably justified to assume that this tree was an important dry season plant resource.

The study area had a dry season from May until September and *Celtis* and *Dialium* may represent some of the 'keystone' resources of tamarins in this area, but insufficient data were collected to confirm this. Additionally, during the dry season when food resources are at their most limited, tamarins may utilise food resources not normally relied upon (Garber, 1993b). These resources include the exploitation of nectar from flowers (Garber, 1988b, 1993b; Goldizen *et al.*, 1988; Peres,1986, 1991; Soini,1987; Yoneda, 1984a) and naturally occurring exudate sources, such as the exudate from *Parkia* (Buchanan-Smith, 1990a,1991a; Peres,1991; Pook & Pook,1982; Terborgh, 1983). The present study found that *S. fuscicollis* used at least two sources of nectar, *Ochroma lagopus* and *Chorisia speciosa*. These two species of flower were not found in other studies (e.g. Buchanan-Smith,1990a; Yoneda,1984a) and probably represent two previously undocumented tamarin nectar sources. *S. labiatus* were not observed consuming nectar from flowers, but were seen to be eating what was thought to be exudate, from the fruits of *C. speciosa.*

Observation of *C. speciosa* exudate was slightly problematic. It was clear that the fruit itself was not being eaten, but it was not possible to be definite as to whether the tamarins were eating exudate, or were consuming insects. However, they were assumed to be eating exudate for three reasons : a) the tamarins visited the tree on an almost daily basis, for a period of some 10 days, where they followed a systematic route and did not carry out much insect foraging en route. b) when they harvested the fruit they always used their mouths to consume the 'exudate' and moved about the various fruits - this was not the normal 'seize and capture' insect foraging technique of *S. labiatus* (Pook & Pook,1982; Yoneda,1984b), and c) fallen examples of this fruit were found to have resinous exudate on the outside (possibly caused by insects). This led me to believe that this fruit was an exudate source for *S. labiatus.*

In summary, the tamarins in the present study consumed a similar range of resources to those reported in other studies, with *Moraceae* being the most commonly consumed plant family (e.g. Yoneda, 1984a). They were utilising many of the main reported genera of plants, and were probably also dependent on 'keystone' fruit resources, nectar sources, and exudates during the dry season. Their selected range of plant resources was not unique amongst Neotropical primates, but like other tamarins, their reliance of key resources probably was (Terborgh,1983; Garber, 1993b).

2.10.6 *Plant foraging strategies.*

Most studies, like the present one, have found that tamarins predominantly feed on small sized fruit resources situated at the trees terminal branches. This has been shown in various tamarin species ; *S.midas* : Fleagle & Mittermeier, 1980; *S. fuscicollis* : Garber, 1986, 1987; *S.geoffroyi* : Garber, 1980a; and *S.imperator* : Terborgh, 1983. Both species in the present study were found to use grasping strategies to exploit fruits, and Garber (1993b) has argued that differences between species are less apparent during fruit foraging. Snowdon & Soini (1988) indicate that *Saguinus* species often take small fruit species directly by their mouths, medium fruits are taken by hand, and are consumed while being held, while larger fruits are eaten where they hang. Also Garber (1993b) showed that *S. mystax, S. fuscicollis* and *S.geoffroyi* all concentrated fruit feeding on small (< 5cm) and medium (<10cm) sized branches, located at heights of 16m+, and most often used grasping and sitting postures.

These descriptions fitted well with the foraging strategies outlined in the present study. Both *S. labiatus* and *S. fuscicollis* used grasping strategies on thin terminal branches to extract the small amount of ripe fruits at the periphery of fruiting trees. The also used sitting where appropriate, and consumed the different sizes of fruits in the manner described by Snowdon & Soini (1988), often consuming the seeds of smaller fruits. Garber (1986) has demonstrated that seeds consumed by tamarins have a high germination rate, so these animals may be important seed dispersers.

One other interesting finding of the present study, was that the ten shared plant resources were often consumed by *S. labiatus* before *S. fuscicollis*. This is not generally reported in *Saguinus* mixed-species groups (e.g. Pook & Pook,1982; Terborgh,1983), but the position of the mystax group being dominant over the *S. fuscicollis* is well documented (e.g. Buchanan-Smith,1989; Heymann, 1990b; Pook & Pook,1982). However previous studies fail to mention any systematic, serial feeding pattern, where the more dominant congener eats first, and the other species has to wait until all or most of the dominant species are finished. Terborgh (1983) mentioned that *S. fuscicollis* and *S.imperator* fed in either the same tree, in serial, or in parallel, depending on the size of the resource being exploited (i.e. big resource = no competition ; smaller resource = competition). Both Peres (1991) and Heymann (pers comm.) found that for *S. mystax and S. fuscicollis,* the species occasionally fed in parallel when exploiting large resources, but *S. mystax* being the more dominant they could expel their congeners from a desired resource. They also found that *S. mystax* were frequently first to reach the large resources. For *S. labiatus* and *S. fuscicollis,* Yoneda (1984b) indicated that the two species did not generally eat in the same tree, at the same time, but does not state which species was first to eat. Buchanan-Smith (1989) indicated that *S. labiatus* took the lead in the mixed groups, and the first *S. fuscicollis* entered feeding trees as the last *S. labiatus* left. So from my observations and the other studies outlined above, it is clear that *S.labiatus* have priority of access to large resources and are often the first to enter such feeding trees, with *S.fuscicollis* only entering when their congeners are leaving, but in most cases there were no direct interactions between the species.

2.10.7 Height preferences.

In common with other studies of *Saguinus* mixed-species troops, there were both similarities and differences between the species (e.g. Norconk,1990b; Pook & Pook,1982; Terborgh,1983). Although not enough data points were collected to make detailed comparisons for all activities, some general patterns were found. Also, these findings must be viewed with caution, as visibility of small New World primates may be related to their mean height in the forest (Ferrari & Rylands, 1994).

S. labiatus was usually found at a higher level of the forest than its congener, and this was found in other studies of these species (Buchanan-Smith,1989,1990a; Cameron *et al.*, 1988; Pook & Pook, 1982 ; Yoneda,1981, 1984b) and also in other *Saguinus* mixed-species troops, where *S. fuscicollis* was always found at a lower mean height (Norconk, 1990b; Peres, 1991,1992a; Terborgh,1983). The two species were found to consume fruit at a similar height, and this reflects the large overlap in fruits consumed by both species (see earlier). Once again other studies have shown this similarity in mean fruit foraging height (e.g. Norconk,1990b; Yoneda,1981; Peres, 1991). Insect foraging on the other hand shows an important difference between the species.

The two species not only forage for insects at different heights (see Chapter 1; Section 1.6), they also forage by means of different styles (Yoneda,1981,1984b). This has recently been described in detail by Garber (1993b), who categorises 3 different *Saguinus* insect foraging strategies. He describes "pattern 1" as being typical of *S.geoffroyi,* "pattern 2" as being representative of the *S. mystax* group, and "pattern 3" as being representative of *S. fuscicollis.*

The salient characteristics of pattern 2 are : insects are exploited from leaves and branches on the middle and lower canopy, and the tamarins use visual scanning, stealth and quick seizure, to gain a food item. These descriptions fit almost exactly with the description in the present study and in other studies of *S. labiatus* (Buchanan-Smith,1990a; Yoneda,1984b). Pattern 3 : Garber (1993b) argues that all studies of *S. fuscicollis* have demonstrated a concentration of insect foraging on large, hidden prey. *S. fuscicollis* has been shown to forage predominantly on moderate to large sized trunks, and most foraging is conducted at a height of 6 metres or less (Norconk,1990b; Soini,1987; Terborgh,1983; Yoneda,1984a). In the present study a similar pattern was found, whereby *S. fuscicollis* used a manipulative, extractive style, at an average height of less than 5 metres.

Both species therefore show a convergence in the mean height used while fruit foraging, but diverged greatly in the mean insect foraging height. This probably reduces competition between the species, as insect foraging accounts for a large part of both species behavioural repertoire (e.g. Peres,1992a; Yoneda,1984b). There is also evidence that *S. fuscicollis* takes a different set of insects than the *S. mystax* group (Garber, 1993b; Peres, 1992a; Yoneda,1984a). Thus, although the potential for competition between species is high for fruit resources, the differences in insect foraging may allow the two species to reduce the overall potential for inter-specific food competition and to co-exist amicably. Peres (1991) found that *S. mystax* flushed prey downwards to *S. fuscicollis*, at a negligible cost to themselves. This was not observed in the present study.

The overall height difference and differences in substrate preference are probably related to the large amount of locomotion data in the current study (61% of all activity data points were concerned with locomotion). This left insufficient data points to examine other behaviours separately and overall data would be totally based on locomotion. Therefore only substrate use and height preference during locomotion is examined.

2.10.8 Locomotion in mixed-species troops.

In the present study the two species were shown to differ significantly in their preferred style of locomotion. *S. fuscicollis* relies upon vertical clinging and leaping for over 25% of locomotion, while *S. labiatus* only uses this method for less than 5% of locomotion. *S. labiatus* showed a reliance on quadrupedal running and walking, which *S. fuscicollis* used far less frequently. The species locomoted at a significantly different height, with *S. labiatus* being found at a higher height than its congener.

The increased use by *S. fuscicollis* of vertical clinging and leaping at lower levels of the forest appears well documented (e.g. Garber,1991; Moynihan,1976; Soini,1987; Yoneda,1984b), as has the prominence of quadrupedal progression in members of the *S. mystax* group (e.g. Buchanan-Smith, 1990a; Norconk,1990b).

Recently, Garber (1994) has argued that the main method of travel in all tamarin species is quadrupedal progression (i.e. walking, running & bounding). He further argues that although *S. fuscicollis* are frequently reported to use vertical clinging and leaping, this accounted for only 6%

of travel in his study group. This questions the importance of vertical clinging and leaping in the present study, and as there were only a small number of observations, it is possible that the current sample contained a disproportionate number of conspicuous activities such as vertical clinging and leaping. On the other hand, the importance of vertical clinging and vertical clinging & leaping by *S. fuscicollis* during insect foraging is well documented (e.g. Garber,1993b; Pook & Pook,1982; Yoneda,1984b) and so any difference between the species is important. Finally, Garber (1991: 220) used an extremely stringent definition of locomotion, which involved "coordinated group movement or any non-foraging/non-predator avoidance activity, during which an individual crossed between the crowns of adjacent trees". This definition obviously precludes the frequent movements during foraging and other activities and would necessarily underscore the amount of vertical clinging & leaping by *S. fuscicollis.* Most other studies, including the present one, would usually count locomotion as a physical displacement of the animal. This may partially explain the increased importance of vertical clinging & leaping in other studies when compared to Garber's (1991) study. Overall, however, the important comparison is between the species in the present study, as the same behavioural classification was used for them, and on this basis the relative differences were valid.

The mean travel height for members of the *S. mystax* group has generally been shown to be higher than that of *S. fuscicollis* (e.g. Buchanan-Smith,1990a; Peres,1991). The present study indicated that *S. fuscicollis* locomoted predominantly in the 5-10 metre area of the forest, and this was similar to other studies, both in single species groups (e.g. Soini,1987) and in mixed-species troops (e.g. Yoneda,1984b). This suggests that they are not 'forced' to occupy the lower areas of the forest, but have evolved characteristics such as small body size and relatively long hindlimbs & forelimbs (compared to other tamarins; Garber,1991), which allow them to occupy this niche (Garber, 1993b, 1994). The large sized vertical trunks found in this area necessitate the use of their claw-like tegulae to support their bodyweight on substrates that they could not grasp in their hands and feet (Garber,1991). These tegulae allow the *S. fuscicollis* to move up and down and between large substrates, and they can use vertical clinging & leaping to locomote effectively in this area of the forest.

S. labiatus were found at a higher level of the forest, and this was probably related to their predominant use of quadrupedal progression, which was usually conducted along fairly large branches, in the lower and middle canopy area. This was found in all members of the *S. mystax* group (e.g. Buchanan-Smith, 1990a; Garber,1991; Norconk, 1990b) and for other tamarin species (e.g. Fleagle & Mittermeier,1980; Garber, 1980a; Garber & Sussman, 1984; Neyman,1978). Garber (1994) has argued that this form of locomotion characterises *Saguinus* travel, and in the present study it is the main travel method for *S. labiatus.* The mean travel height in the present study corresponded with the lower and middle canopy areas, and this is probably the most efficient method to locomote on the substrates found in this area.

2.10.9 Substrate use during locomotion.

Both species used all three orientations of substrates, but they used small and large sized substrates more frequently than medium sized substrates. A similar pattern was found in *S. mystax* and *S. fuscicollis* (Garber,1991). Few studies have systematically examined substrate use, but Norconk (1990b) demonstrated that *S. fuscicollis* used larger substrates more than its congener.

In the present study, the distribution of substrate size to height showed that *S. labiatus* predominantly used small branches in the 15-25m height band, whereas *S. fuscicollis* used mainly large substrates at a height of 0-10m. Also, the interaction between orientation and size of substrate produced a different pattern in the species. The highest ranked pairing for *S. labiatus* was small oblique substrates, but for *S. fuscicollis* it was large vertical substrates. These differences are intrinsically linked to the main locomotory styles used by each species, and within these pairings each species used their most common locomotory style, vertical clinging & leaping for *S. fuscicollis* and quadrupedal progression and leaping for *S. labiatus*.

In summary, substrate use during locomotion was different for each species and corresponded to the vertical stratification of these species and the type of substrates present in each area. *S. fuscicollis'* use of large trunks during locomotion was tied into their use of vertical clinging and leaping to locomote, as by using their claws and elongated forelimbs, on these vertical substrates they can utilise substrates which are otherwise too large to use. This allows them to utilise these trunks for insect foraging, a niche which is not used by their congeners, and to lessen interspecific feeding competition. On the other hand, *S. labiatus* used quadrupedal progression and leaping onto small oblique substrates which they grasped and "scrambled over", and this was mainly in the middle and lower canopy area, where they concentrate on fruit and insect foraging. The two species were also shown to differ in both locomotory style and substrate use, both of which were efficient methods for their particular area of the forest.

2.11 Summary.

Mixed groups were common throughout the study area and most groups of both species were thought to be part of mixed-species troops.The mean group sizes found in the current study were within the 'normal' range of sizes. *S. labiatus* mean group size and maximum group size were larger than those for *S. fuscicollis*. Births, and subsequent lactation were probably centred around the period of peak fruit production. Both species shared many plant resources and fed mainly in a serial manner, with *S. labiatus* feeding before *S. fuscicollis.*

S. labiatus and *S. fuscicollis,* in common with other tamarin species, relied upon key resources during the dry season, including nectar and plant exudates. Also, *S. labiatus* were usually found at a higher level of the forest, except during the exploitation of their shared fruit resources.

The species differed in both preferred area of forest to locomote upon, and consequently in favoured method of locomotion. *S. labiatus* locomoted predominantly by means of quadrupedal progression in the lower and middle canopy areas of the forest, where most substrates were oblique and horizontally orientated. *S. fuscicollis* alternatively, progressed by means of vertical clinging and leaping, using its elongated arms and nails to grip onto the many large vertical trunks found in the lower area of the forest.

Chapter 3 : Methods for the Study and Formation of Captive Mixed-Species *Saguinus labiatus* and *Saguinus fuscicollis* Groups.

3.0 Introduction.

One problem encountered while studying the costs and benefits involved with association in mixed-species groups in the wild, is that where the two species are sympatric, they are seldom found monospecifically (see Chapter 1). This is largely because the tamarin associations are extremely coherent and long lasting, and are based around shared territories which contain essential plant resources (e.g. Peres, 1991). Many plant species are shared between the associating species, and territories are concurrently defended by both species against conspecifics (e.g. Garber, 1988a; Chapter 2). Where studies have been conducted for lengthy periods, it has become apparent that associations between specific groups may last for a number of years (Terborgh, 1983). Also, it is widespread over the whole area where tamarin species are sympatric, with most or all of the individual groups of both species forming associations. For example, Terborgh (1983) found only one single case of a monospecific *S. imperator* group, and this was only a temporary condition, as they soon formed a mixed group with an available group of *S. fuscicollis.* So it is clear that in the wild, monospecific groups of tamarins are rarely encountered in the areas where species are sympatric.

Association is an adaptive and lengthy occurrence, that must involve the participants in a series of costs and benefits (e.g. Peres, 1991). In order for the association to develop, the benefits accrued by the members of a polyspecific group must outweigh the costs. The main areas of proposed benefit are detection and avoidance of predators, defence against predators, increased encounter rate with food and defence of food resources. On the other hand, costs such as increased conspicuousness and increased feeding competition may occur (see Chapter 1). In order to adequately test predictions based upon the behaviour of mixed-species tamarin groups, it is essential to be able to determine what possible differences occur between single species groups and mixed-species groups. This is because it is not possible to accurately determine the various costs and benefits involved in an association, unless it can be shown that the behaviour of the individuals associating is influenced by the association. Captivity uniquely gives the experimenter a chance to manipulate and control the conditions, and to look at changes between single species and mixed-species groups. This has to be reconciled with the idea that captivity brings about its own disadvantages : groups are formed artificially, group size is manipulated, animals are enclosed and are free from actual predation. However, the main research theme centred on similarities and differences between the species, and as these disadvantages are equally applicable to both species, then any behavioural findings may be robust. Also, a specific attempt to compare some pertinent aspects of behaviour in captivity and the wild will be addressed in the next chapter, in order to examine the ecological validity of captive mixed-species groups. The remainder of this thesis will concentrate on studying the behaviour of single species groups of *S. labiatus* and *S. fuscicollis*, the subsequent behaviour of mixed-species groups and an attempt to evaluate some of the costs and benefits involved in association.

3.1 Captive tamarin groups.

Despite the close association found between these monkeys in nature, most captive environments house just one species in any enclosure. Therefore it was very simple to compare the behaviour of single species groups. However, in order to study the associations in more detail, it was necessary to formulate a plan to create mixed-species groups of tamarins in a captive setting. The idea seemed to be a novel one - although some pairings of different species of primates had been mixed intentionally (e.g. Poole,1990; personal obs.) and accidentally (Stronge, personal comm.), there seemed to have been very few systematic attempts made to introduce groups of species that were both sympatric and that formed associations in the wild. For example, Xanten (1990) formed mixed-species groups of *Cebuella pygmaea* and *Callicebus moloch*, *Leontopithecus rosalia* and *Callithrix geoffroyi* as well as mixing primate species with non-primate species. A successful mixing attempt was considered to be one which settled down with little signs of distress or injurious behaviour to the participants, but such success was very limited. This may have been because Xanten did not make any attempt to mix species that generally associated in the wild (see Chapter 1 for details of associating species), and attempts to mix *Saguinus labiatus* with other primates led to the conclusion that they were "rather aggressive" and "may not mix well with other tamarins". Indeed, no details were given of any attempts to mix tamarin species together. Baker (1992), in a review of primate mixed-species exhibits, describes a series of such groupings, but once again the cases outlined show no attempt to mix together species which form associations. Finally, Xanten (1992) detailed a further set of mixed-species exhibits, but once again there were no attempts to systematically mix species which are known to form stable associations in their natural habitat.

There is an unpublished report of a mixed *S. labiatus* and *S. fuscicollis* group at Tierpark Ueckemunde in Germany (Heymann, pers. comm.), however no specific details are known. This means that the only reported case of a mixed-species group found in captivity, prior to the present study, was reported by Heymann & Sicchar Valdez (1988). They studied a wild caught group of 5 *Saguinus mystax*, and 6 *Saguinus fuscicollis*, held at Iquitos, Peru, in a cage measuring 9 x 13 x 2.5m. This group was stable, and lived in relative harmony, leading to the conclusion that it was possible, at least in principle, to keep a mixed-species group of tamarins in captive conditions. However, this mixed group was made up of individuals that were wild caught, and no details were given of the method used to form the group. Therefore it was not clear whether or not mixed-species groups of tamarins could be formed in captivity.

Section 3.A : An attempt to create a captive mixed-species tamarin group.

After enquiries, it was found that Belfast Zoo was the most suitable place to plan, design and carry-out a study of a captive mixed-species group of tamarins. The initial plan involved an attempt to create a stable mixed-species group of *S. labiatus* and *S. fuscicollis* in captivity. In order to be considered a success, at least in the short-term, it was deemed necessary for the individuals involved not to show any fighting or injurious behaviour between them, nor demonstrate any visible signs of stress or poor health. This was by necessity a subjective measure, but it reflects a short-term goal for measuring success. A long-term assessment should include parameters such as births and mortality and would need to last far longer than the duration of the present study.

3.2 Methods.

3.2.1 Animals, housing and husbandry.

The study commenced in July 1992, at Belfast Zoological Gardens, Belfast, Northern Ireland. After careful consideration of all the relevant factors, it was decided to make use of an off-exhibit area, in order to reduce "stress" on the animals, and have generally undisturbed conditions within which to work. Initially, the zoo had in its collection, 3 groups of saddle-backed tamarins- *Saguinus fuscicollis weddelli,* and in addition were also willing to acquire some red-bellied tamarins- *Saguinus labiatus labiatus*, with which to form the mixed-species groups. Plans were made to construct a new (temporary) enclosure for the study. The two end cages of the old marmoset compound were selected to house the new groups of tamarins, and the new enclosure was to be built around these cages.

These two cages and the ones that the *S. fuscicollis* had previously been housed in can best be described as a "traditional" indoor/outdoor marmoset enclosure. The right side end cage consisted of an indoor area of approximately 2 x 1.75 x 1.5m, furnished with a woodchip covered concrete floor, a shelf to rest and sleep upon and a heat-lamp to warm it, and also a 1.9 x 1.8 x 2.3 m outdoor, mesh covered area, furnished with a few (approx. 8) small, medium and large sized branches. The outside of the outdoor cage that was adjacent to the new cage, was screened from the new cage by means of a plastic screen, stopping visual access from the bottom of the new cage. Visual access could occur by means of looking down through the roof of the *S. fuscicollis's* outdoor cage. The other end cage had a smaller (1.65 x 1.55 x 1.5m) similarly furnished indoor area but a larger outdoor area (1.95 x 1.55 x 3.5m) again containing a few branches (approx. 12) and a woodchip covered floor (see Figure 3.A [I]).They were housed beside other callitrichid species (e.g *Cebuella pygmaea, Saguinus imperator, S. fuscicollis, S. oedipus, S.midas*), and Goeldi's monkey, as well as several bird species (e.g. macaws, parrots, ibis).

Two *Saguinus fuscicollis,* were selected to be mixed with *S. labiatus.* These consisted of a wild-born male and a young captive born female (see Table 3.A for details). This pair were chosen due to the male being wild caught, as it was conceivable that he might have had prior experience of being in mixed-species groups. This new pair was introduced and paired on 11th of August 1992, and placed into the right side end cage. This cage will be referred to as the *S. fuscicollis* Home cage.

Two *Saguinus labiatus,* one male and one female were obtained from Chester Zoo, at the end of July 1992, and they were paired at this time (for details of ages etc. see Table 3.A). They were placed in the left side end cage, now referred to as the *S. labiatus* Home cage (see Figure 3.A[I]).

Table 3.A : Age, sex and identity of tamarins studied at Belfast, 1992.

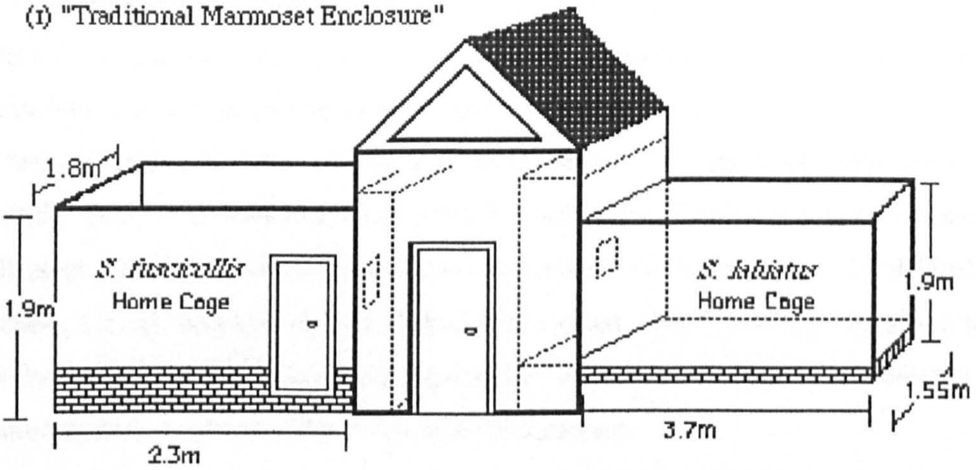
Group SF1			Group SL1		
Saguinus fuscicollis			*Saguinus labiatus*		
Sex	Age[1]	I.D	Sex	Age[1]	I.D.
male	8yrs[2]	195	male	2yr 9mth	664
female	2yrs 1mth.	489	female	1yr 7mth	665
Date paired : 11/8/1992			Date paired : 23/7/1992		

[1] age in years and months, at start of study.

[2] as wild caught, age is only approximate.

The new enclosure was built during July and August 1992, with a wooden framework and mesh netting. Within the new cage, and adjacent to the two home cages, there was a small semi-circular area of shrubs (approximate diameter of 3m), containing one palm tree growing up to a height of approximately 4 - 5 metres. Outwith these shrubs, the ground was sloping and covered in bare tarmac. The framework stretched from the furthest point of *S.labiatus* home cage until the end of the *S.fuscicollis* home cage, spanning their whole length. As the frame was built on a slope, the two ends were of a different size (Figure 3.A [II]).

(I) "Traditional Marmoset Enclosure"



Inside areas : S. fuscicollis 2 x 1.75 x 1.5m : S. labiatus 1.65 x 1.55 x 1m.

(II) New Outdoor Area

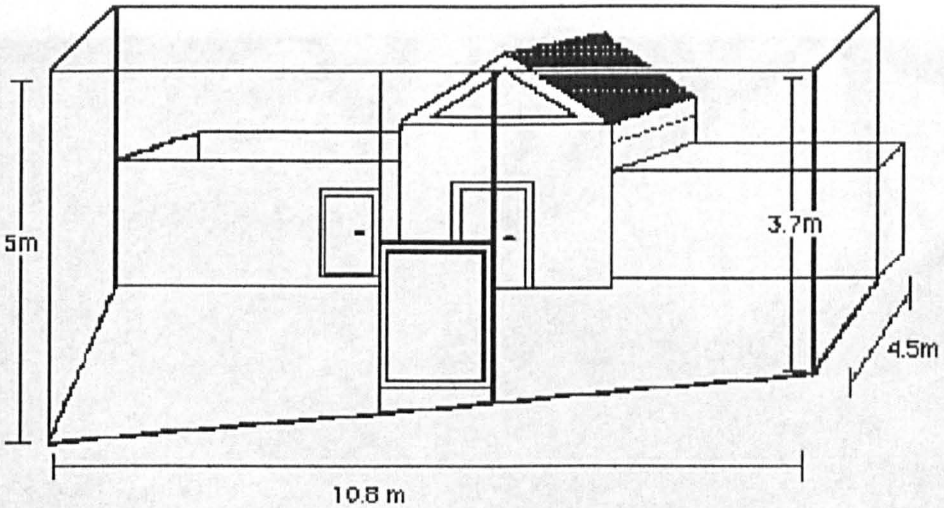


Figure 3.A : Dimensions and plan of mixed-species cage system at Belfast zoo.

The frame was covered with a mixture of both 1" square netting and 1cm square plastic pond netting, and this was attached firmly to the existing framework. Plastic guttering on the building was covered with plywood in order to prevent the monkeys escaping through it.

This area was furnished with a variety of cut branches, of various sizes, built into in a network and with thin branches intermingled together, in order to create an artificial "canopy" (see Plate 3). These branches were fixed together, to the wooden framework, and to the tarmac, by means of wire and nails. Large sized tree-trunks were placed horizontally, to give the monkeys a solid "runway" with which to enter the area. Most areas of this cage were connected by means of horizontally interlinked branches. Access to the outdoor area, from their respective home cages, was different. For *S. fuscicollis* access was via a preexisting large door (1.8 x 0.78m) and for *S. labiatus,* a small doorway (0.22 x 0.28m) was created. The "runways" were near to the doors, so that the monkeys could have a solid substrate on which to enter their new enclosure, and so to minimise fear and uncertainty due to the new environment.

Plate 3 : Network of branches in new enclosure.

3.2.2 Introduction to the new area.

The animals were introduced to the new cage system one species at a time. While one species was allowed access to the new outdoor area, the other species was closed into the indoor area of their home cage. This meant that the two species were in auditory and olfactory contact but not in visual contact. This strategy was adopted as it was decided to examine the behaviour of each species individually, with the minimal of effects of the other species. Between 13th and 20th August 1992, each species was independently given access to the outdoor area, for approximately the same amount of time. This process allowed the animals to familiarise themselves with the new surroundings and to lay down scent marks on this "territory". Access was initially limited to 1 or 2 hours for each species so that the first species to enter the area would not have sufficient opportunity to scent mark over the whole area.

Initially both species were very wary of the new area and frequently scent marked and alarm called, but these behaviours decreased in frequency over the course of initial familiarisation period. The new enclosure was divided up and visually marked into separate areas and a general note was taken of where the animals were seen to venture (Figure 3.B). After some 15-20 hours of access for each species it was decided that most areas of the enclosure had been used and so it was possible to begin the first sampling part of the study

3.3 Visual introduction of species.

After the familiarisation period, carried out under visual separation, it was decided to allow the species the opportunity to see each other. Firstly it was necessary to measure a baseline estimate of "interest" in the other species, during visual encounters. As the familiarisation period gave the individuals an opportunity to look at the other species' home cage, while the subjects were locked inside, it was necessary to formulate a method for doing this. It was first appropriate to screen the *S. labiatus* home cage from view (by means of opaque orange plastic) as was the case with the *S. fuscicollis* home cage (see Figure 3.C). The *S. fuscicollis* home cage was additionally screened by the orange plastic, in an attempt to standardise the conditions (e.g. rustling of plastic, etc.).

This meant that the animals out in the new cage had to climb high and look down through the roof of the appropriate home cage, in order to view inside it. This was the achieved, by means of the animal wishing to view, climbing high (2.5m or higher) and looking down into the other species' outdoor area (Figure 3.C). Both species now had a comparable way of looking into each others' home cages and this gave the observer an opportunity to gauge the level of interest of one species in the presence of the other species' in their home cage.

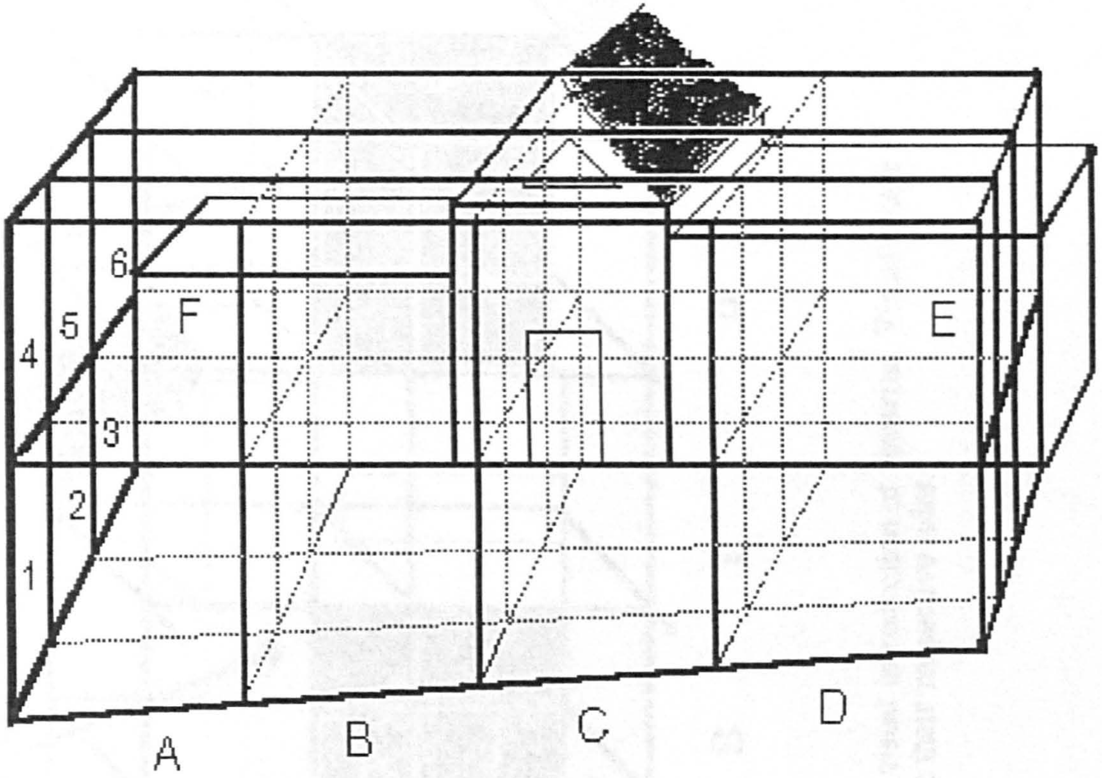


Figure 3.B : Areas of cage used to define use of space.

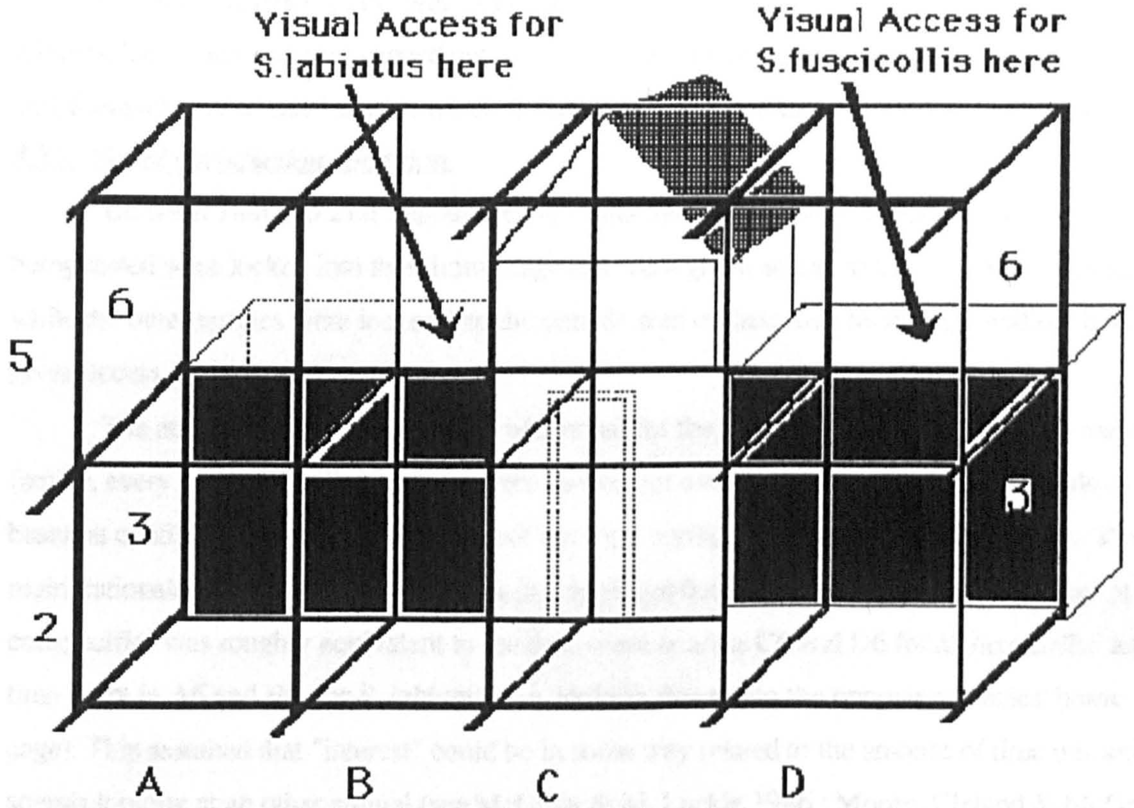


Figure 3.C : Set-up for visual introduction of tamarins. Visual access is by 'looking down' from their respective sides.

3.3.1 Baseline condition.

During the daily observation periods (i.e. morning 0900-1300h ; afternoon 1300-1600h), I examined the use of space in the absence of conspecifics, using instantaneous scan sampling (Martin & Bateson,1986) of the area of the enclosure used by both the individuals, every three minutes. This condition was carried out as a single species condition and it involved visual isolation and gave a baseline with which to compare with the visual introduction condition.

3.3.2 Visual introduction condition.

Between 18th and 21st September the visual introduction was carried out. The animals being tested were locked into their home cage and were given access to the new outdoor area, while the other species were locked into the outside area of their own home cage without being given access to the new cage.

The animals' position in the cage was noted for the species being tested, for both male and female, every 3 minutes. Observations were carried out over exactly the same time periods as the baseline condition, and in the same manner but for a period of 2.5 hours for each subject. The main rationale behind this was that it was assumed that the amount of time spent "looking" at their conspecifics was roughly equivalent to the time spent in areas C6 and D6 for *S. fuscicollis* and the time spent in A6 and B6 for *S. labiatus* (i.e. looking down into the opposing species' home cage). This assumed that "interest" could be in some way related to the amount of time one animal spends looking at an other animal (see McGrew & McLuckie,1986 ; Moore, Cleland & McGrew, 1991) and this could give an estimation of active interest between the species. Comparison between the baseline and visual introduction conditions, led to an indication of the change in interest to the home cage due to the presence of the other species. Also, both species could be compared in terms of their relative interest in their conspecifics, as well as for sex differences in interest. In addition, the behaviour of both species, for example scent marking and alarm calling and aggression was noted, ad libitum, during these visual encounters.

3.3.3 Results.

The species were compared in simple terms, namely the amount of time spent in close visual contact with the other species' home cage. This involved the proportion of time spent by *S. labiatus* in areas A6 & B6, and the time spent by *S. fuscicollis* in C6 &D6 (Table 3.B).

There was a general increase in the amount of time spent in close contact with the home cage area of the other species, indicating a general tendency to 'observe' the other species. This was larger for the *S. fuscicollis*, but overall both species were seen to be moderately interested in each other, and there was no aggression between them.

Table 3.B : Percentage of occasions spent in close visual contact during baseline and visual introduction trials.

Baseline (2nd species not present)		
S. fuscicollis	Male 12%	Female 7%
S. labiatus	Male 1%	Female 2%
Visual Introduction (2nd species present)		
S. fuscicollis	Male 32%	Female 38%
S. labiatus	Male 5%	Female 14%

3.4 Mixing the species.

Due to the fact that no overt aggression was shown towards the species when in visual contact (i.e. no attempts to attack the other tamarins were observed for either species), meant that I felt confident that the two species could be mixed amicably. The first step involved the removal of the plastic screens on both the home cages, and this allowed a closer view of each species.

As during this stage, there were no signs of aggression between the species, I decided to mix them. There were some limited attempts at contact between the species, but none of them looked to be of an aggressive nature. Also, the large size of enclosure and the potential for each species to abscond, negated fears for the safety of the animals being mixed.

3.4.1 Initial attempts at mixing.

On the 22nd September 1992, during the afternoon, the two species were both simultaneously given access to the large outdoor area, but were both initially denied access to their respective indoor areas. Only data relevant to the establishment of a stable association (e.g scent marking, interactions and aggression between the species) was noted, ad libitum.

The mixing unfortunately did not go well. Initially both species remained in their respective home cages, for 5 - 10 minutes, then the *S. labiatus* advanced out of their area. Then when the *S. fuscicollis* caught sight of the *S. labiatus* they reacted in an aggressive manner. Both the male and female *S. fuscicollis* launched an attack on both the *S. labiatus*, leaping at them, teeth bared and trying to "wrestle" with them. The *S. labiatus* retreated abruptly away from the attacking tamarins, and fled to their own home cage. Large amounts of alarm calling occurred, by both species, and the *S. fuscicollis* additionally scent marked (mainly anogenital) frequently. The *S. fuscicollis* followed the *S. labiatus* into their home cage and aggressively displaced these animals from their home cage. There were no obvious signs of injury to any of the monkeys. Both the invading animals scent marked throughout the area, alarm calling profusely and trying to attack the *Calllithrix jacchus* male occupying the adjacent cage. This attempt to attack the common marmoset, lasted for 15 minutes and was only terminated when the marmoset was shut into its own indoor area. During this time, the two *S. labiatus* mostly stayed at the opposite side of the large outdoor area but gradually came closer to their own home cage (i.e. Areas C2 & 3).The *S. labiatus* were of a much calmer disposition than the *S. fuscicollis* and made no attempt to enter their own home cage. Eventually the *S. fuscicollis* left the home cage. As they entered the large outdoor cage, they quickly noticed the *S. labiatus* and reacted by alarm calling and immediately launching themselves at the 2 *S. labiatus*. The female quickly rushed into her home cage and was given access to the indoor area. The male on the other hand, ran to the opposite end of the cage and absconded in the thick bushes there (i.e. Areas A2 & 3), where he remained hidden until the *S. fuscicollis* were placed in their indoor area. He had remained silent and motionless during all this time and only left the bushes very slowly and cautiously. The female gave many short "contact calls" and was very agitated by the male's absence. Once it was established that there were no visible signs of injury, they were both allowed into their own home cage. For the remainder of the day they were allowed to enter the new outdoor cage and view the *S. fuscicollis*.

3.4.2 Problems and solutions to mixing.

In light of this unsuccessful attempt, some changes to the procedure were necessary. The following were considered important.

a) The *S. fuscicollis* appeared to consider the new area to be their territory and aggressively "defended" it.

b) The presence of the male *Callithrix jacchus* was detrimental to the mixing as the *S. fuscicollis* acted aggressively to it.

c) The *S. labiatus* were acting submissively to the *S. fuscicollis*, contrary to the expected dominance order (i.e.*S. fuscicollis* always submissive to its congeners cf. Terborgh,1983; Heymann,1990b ; Norconk,1990b).

d) Possibly not enough visual access time was given between the species, so they were not used to each other's presence.

e) The *S. fuscicollis* may have been atypical in that they were more aggressive than the *S. labiatus*, or alternatively the *S. labiatus* may have been more submissive than usual.

f) I may have been too quick to separate the animals, and it could have been better to let them fight, to establish dominance.

g) The *S. fuscicollis* were the main aggressors, and may need to be replaced.

As the possibility of being able to produce a mixed-species group of tamarins in captivity was still assumed to be viable, it was believed that implementing some procedural changes would allow the mixing to progress. The *Callithrix jacchus* male was the easiest problem to solve ; he was simply translocated to an empty cage further down the complex. The idea of the *S.*

fuscicollis claiming the territory was more difficult as both species had approximately the same amount of access to the new area and both species had observed the other species in the new area. The fact that the *S. fuscicollis* had other groups of their own species nearby and that they had scent marked much more often than the *S. labiatus*, may have been an indication of the territoriality that was to come. But the driving out of the *S. labiatus* from their own home cage was definitely unexpected. The main proposal to counteract this would be for the *S. fuscicollis* to get better acquainted and "used" to the presence of *S. labiatus* in the new area. Basically the plan was to force the two species to be in visual contact for more time than they previously had done, and this could be achieved by moving the *S. labiatus* one cage down (i.e. where the *Callithrix jacchus* had been) and to move the *S. fuscicollis* into the cage where the *S. labiatus* had been (Figure 3.D). Both species could be given access to the new area, and at other times they would be in visual contact (i.e. when both in their respective outdoor areas). Also it was considered feasible to place one species in a small "satellite cage" and to place this within the other species outdoor cages, to allow a more intimate level of interaction.

This was thought to enable the solving of the "not enough visual access" problem, as well as solving the "territoriality" problem. It was decided to try a much longer duration of introduction than the first attempt to see if the aggression would subside over this longer time scale. The other option of replacing one or both of the *S. fuscicollis* was considered to be a fairly final move and only to be tried after the failure of all other options.

3.4.3 Familiarisation period.

The two species were allowed to see each other for a period of 3 days (from 25th to 28th September) and during this time they were both locked out into their respective outdoor areas. While the monkeys showed no real aggressive attempts to attack each other it was appropriate to remember that there was no attempts in the first visual introduction period. Nevertheless it was felt that the two species seemed to be getting on better, and so it was decided to try again to mix them.

3.5 Second mixing attempt.

On the morning of 29th September, at approximately 11.20h, both species were given access to their respective outdoor and indoor areas. The large connecting door between the two outdoor areas was removed and both species were allowed free and unrestricted access to both the indoor and outdoor areas. Firstly the 2 *S. fuscicollis* moved quickly into the *S. labiatus* outdoor area and at this time both the *S. labiatus* were also out and initially both sets of animals paid little attention to each other. The two species were much more relaxed than in the previous introduction and no real evidence of distress in either set of animals was noticed.

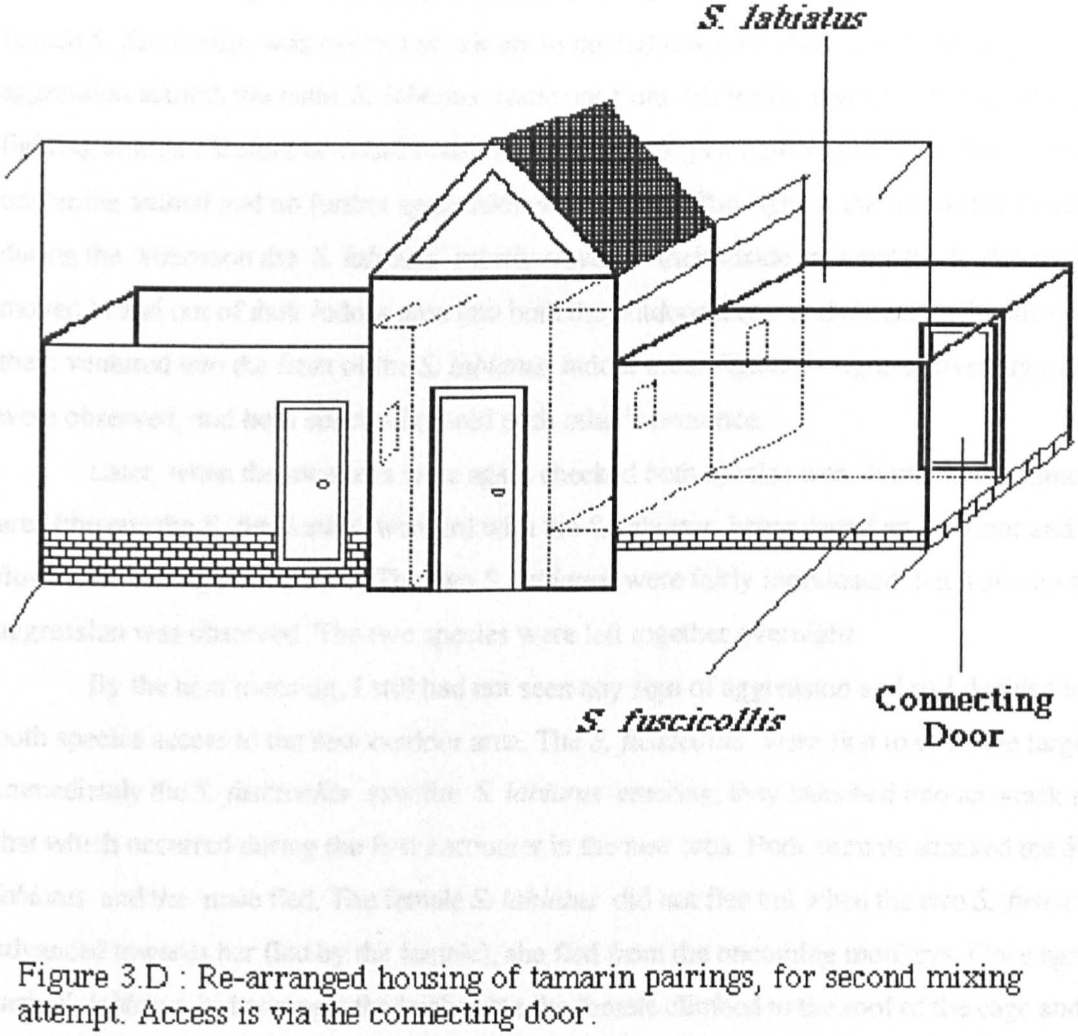


Figure 3.D : Re-arranged housing of tamarin pairings, for second mixing attempt. Access is via the connecting door.

Specifically alarm calls were minimal and no pilo-erection was shown, nor was there any of the aggression shown in the first attempt. Indeed, both females were on the same branch, within about 10 cm apart, ignoring each other. Both pairs were active, but especially the *S. fuscicollis,* and in particular the female. She moved about a lot and was seen to be investigating the new area. Only one aggressive incident was noted between the species. While the female *S. labiatus* was on the ground the male *S. fuscicollis* jumped at her and wrestled with her and the female *S. fuscicollis* was in close proximity to the fighting pair. Almost immediately the aggression started, the male *S. labiatus* came out from his inside area and advanced towards the fighting animals. Before he could reach them, the two *S. fuscicollis* quickly withdrew from the oncoming animal and no further aggression was shown. Throughout the rest of the morning and during the afternoon the *S. labiatus* mostly stayed in their inside area and the *S. fuscicollis* moved in and out of their indoor area into both the outdoor areas and occasionally one or both of them ventured into the front of the *S. labiatus* indoor area. Again no signs of overt aggression were observed, and both species ignored each other's presence.

Later when the monkeys were again checked both species were found in the same inside area (the one the *S. fuscicollis* were in) with the *S. labiatus* being found on the floor and the *S. fuscicollis* sitting on the shelf. The two *S. labiatus* were fairly intimidated, but again no sign of aggression was observed. The two species were left together overnight.

By the next morning, I still had not seen any sign of aggression and so I decided to allow both species access to the new outdoor area. The *S. fuscicollis* were first to enter the large area. Immediately the *S. fuscicollis* saw the *S. labiatus* entering, they launched into an attack similar to that which occurred during the first encounter in the new area. Both animals attacked the *S. labiatus* and the male fled. The female *S. labiatus* did not flee but when the two *S. fuscicollis* advanced towards her (led by the female), she fled from the oncoming monkeys. Once again the male *S. labiatus* hid amongst the bushes but the female climbed to the roof of the cage and absconded behind a vertical support of the cage. Both animals were very intimidated by the presence of the other species and the *S. fuscicollis* were placed back into their outdoor area. The two *S. labiatus* were very nervous and did not return to their own area for a long time. It was decided ultimately that the male *S. labiatus* was more submissive than would have been predicted from observations in the wild, especially when compared to the aggressiveness of the *S. fuscicollis*. Therefore it was reluctantly concluded that the current pairings of species could not be mixed under the present conditions.

As Belfast Zoo at this time only had this single pair of *S. labiatus* it was clear that the *S. fuscicollis* had to be replaced.

3.5.1 New animals.

On the 1st of October it was decided to change the pair of *S. fuscicollis* involved in the association attempts. The new subjects selected were a male and female that were paired only at this time (for details see Table 3.C). The new species were housed in the cage system that the *S. labiatus* were in (i.e. the second cage down) while the *S. labiatus* were in their original home cage. Two nest boxes made from 1/4" plywood, approximate size 25 x 30 x 30cm were placed on the walls of each indoor area, to provide more space for the animals, allowing plenty of room for both species.

Table 3.C Age, sex and identity of new tamarins studied.

Group SF2
Saguinus fuscicollis

Sex	Age[1]	I.D.
male	2yr 3mth	474
female	1yr 2mth	468

Date paired : 23/9/1992

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[1] age in years and months, at start of study.

3.6 Third mixing attempt.

After 3 days it was clear that the 2 species were making no attempt to reach each other through the wire and no overt attempts at contact were seen. It was then decided to mix the 2 species. On the 3rd October, the door connecting the two adjacent outdoor areas was opened and the species were allowed to mix. The *S. fuscicollis* made no attempt to enter the *S. labiatus* outdoor area but eventually the female *S. labiatus* cautiously entered the other outdoor area.There was no physical contact between the two species, although the female *S. labiatus* and female *S. fuscicollis* were very close. No aggression occurred for the rest of the day. The 2 species were wary of each other but did not initiate close contact.

The 2 groups were allowed to mix freely over the proceeding week (i.e. until 10th October) but due to the nervousness of the *S. fuscicollis* when in the presence of the observer, they were only observed periodically over the course of the day. During this time only mild aggression was observed; specifically the female *S. labiatus* exhibited head shaking and alarm calling towards the female *S. fuscicollis* when she tried to retrieve a food item from the dish in the *S. labiatus* indoor area. However, these were only minor incidents, as no direct physical contact, or injurious behaviour occurred. For many of the observation periods the two species were either cohabiting the same area (both indoors and outdoors) or were close to each other, without any obvious interaction between them. All animals were allowed access to the new outdoor area and they all used it, but the *S. labiatus* used it most often.

On October 11th 1992 it was decided to place both species in the same indoor/outdoor area and to give them all access to the new outdoor area. Therefore the door between the adjacent outdoor areas was closed and all animals occupied the end cage system. This set-up was left for 2 days so that the animals were accustomed to their new arrangements.

I was absent from the zoo from November 13th 1992 until 20th March 1993, and although the group remained stable, no formal observations were carried out during this period.

3.6.1 Conclusions.

Mixed-species groups could be formed from captive-born tamarins. It was considered that mixing should be carried out in areas that contain unfamiliar areas for both species, in order to lessen potential territorial conflict. Also, the failure of the first groups suggests that sometimes the behaviour of one or more individual animal may strongly influence mixing success. It was also found that an elaborate visual introduction is not necessary, and the animals can be mixed after a couple of days of being housed next to each other. The successful attempt at mixing occurred quickly and any aggression was only in the predicted direction (i.e. *S. labiatus* > *S. fuscicollis*). Once established, the mixed-species group appeared settled down, and remained stable for at least a few months.

After this initial mixing was carried out, and reported in the literature (Hardie, *et al.*, 1993), it was discovered that another group was formed between *S. fuscicollis illigeri* and *S. imperator subrigsescens* , at Cricket St. Thomas, England. This group was formed in early 1994, and has also been stable, with little aggression between the species (Barathy, pers. comm.). There was also a group formed at the Deutsches Primatenzentrum, Göttingen (German Primate Centre), consisting of a family group each of *S. fuscicollis* and *S. labiatus*. This group was together for a period of approximately 2 months, and the two species co-existed amicably (Epple, pers. comm.). It appears that the present thesis describes the only systematic investigation of captive mixed-species *Saguinus* groups.

Section 3.B : Methods for studying single and mixed-species tamarin groups.

As it was established that mixed-species groups could be successfully formed from captive born animals, it became possible to test the species involved on behavioural measures. Clearly, one major advantage of the captive environment is that it is ideal for experimentally testing the hypotheses regarding the various costs and benefits accrued to each species under controlled conditions. In order to determine how each species is affected by the association, tests can be used to compare behaviour in and out of association.

One way in which to examine the behaviour of captive animals is to examine the way they react to unfamiliar and / or novel objects. Groups of both species could be tested on their responses to the presentation of different classes of objects. Objects are used because they are a variable that can be easy manipulated, and can be controlled across presentations. These objects are not stimuli which are normally encountered by tamarins in the wild, but was hoped that they will elicit species-specific responses which may be related to actual situations in their natural environment. Stimuli can be of various types, and each type of object can elicit the correct type of response for the experiment in question. For example, novel non-threatening stimuli can be presented to the subjects in various areas of their enclosures, and the latency to approach could be used to give a comparison of relative 'curiosity'; this could be useful in establishing the potential benefits each species may gain or give, when encountering novel situations. Another type of presentation concerns threatening stimuli, and these can be used to examine the how both species deal with potential dangers. In addition, objects containing food, and others without food, are used to examine the ability of each species to learn properties related to objects. Species may be initially tested monospecifically and in isolation from each other, and are then mixed and re-tested to see exactly how the association affects their behaviour. Within mixed-species groups, details on interactions, competition, spacing and general behaviour can be recorded.

This allows the further testing of behavioural differences and similarities between the two species, and can help investigation into why the two species associate.

3.7 General methods.

3.7.1 Subjects.

Subjects were groups of two species of tamarin monkeys, *S. labiatus* (red-bellied tamarins) and *S. fuscicollis* (saddle-back tamarins), housed in the "old marmoset house" of Belfast Zoological Gardens, Northern Ireland. All animals were captive born, except one single *S. fuscicollis* male, of unknown origin, who had been imported around July 1984.

Eight groups of *S. fuscicollis* and six groups of red-bellied tamarins were studied over the course of the present study. For *S. labiatus*, five of the groups consisted of a simple male-female monogamous pairing, while the last group was a family consisting of a monogamous breeding pair and their three offspring. Six of the *S. fuscicollis* groups were maintained as monogamous pairs, one consisted of a trio, and the the last group contained a breeding pair and their three offspring (see Table 3.D).

Both family and group composition changed over the course of the study. These details are shown in Table 3.D. Three *S. fuscicollis* died during the course of the study; the original female in group SF2 died while under anaesthetic, and both the male and female in SF4 died. The male died in December 1993, while the female died during February 1994. In *S. labiatus* the male in SL3 was euthanased, due to an unidentified illness which failed to respond to medication. The deceased individuals were replaced (see Table 3.D), except for SF4 where both individuals died, and where appropriate previous observations and experiments were replicated.

Subjects that were originally kept as single species groups, were introduced and mixed with the other species to form mixed-species groups. Once mixed, the subjects were maintained as these mixed-groups, and were housed as such. Table 3.E gives details of groups mixed, date of mixing and approximate time spent mixed at conclusion of study. Overall, the mixing process was successful in the short-term, as only one attempt failed immediately. However, as the cause of injuries to the male in SF4 was not clear, it remains a possibility that inter-specific aggression may have occurred, but there was no direct evidence to confirm this. Only observations over a period of years will determine if the mixed-species groups are a long-term success.

Table 3.D : Details of age, sex and grouping of captive tamarins at Belfast.

SF1	**Adult Male**	**27/7/84**	**#195**	**Adult Female**	**8/6/90**	**#489**
	Daughter	28/11/90	#742	Daughter	28/11/90	#743
	Daughter	28/11/90	#835			
	Infant	28/11/90	#926	Infant	28/11/90	#927
SF2	**Adult Male**	**5/6/90**	**#474**	**Adult Female**	**9/11/90**	**#468**
				(female died 9/5/93 & was changed 1/4/94)		
				Adult Female	**16/3/93**	**#743**
SF3	**Adult Male**	**20/11/90**	**#745**	**Adult Female**	**1/1/82**	**#221**
SF4	**Adult Male**	**28/4/84**	**#265**	**Adult Female**	**1/1/84**	**#222**
	(male died 7/1/94)			(female died 4/4/94)		
SF5	**Adult Male**	**28/11/90**	**#744**	**Adult Female**	**28/4/84**	**#213**
	Infant	4/6/94	#946	Infant	4/6/94	#947
	(Died 26/7/94)					
SF6	**Adult Male**	**5/11/87**	**#217**	**Adult Female**	**26/5/92**	**#778**
SF7	**Adult Male**	**12/11/89**	**#776**	**Adult Female**	**6/1/89**	**#223**
	Adult Son	28/11/90	#779			
SF8	**Adult Male**	**21/2/93**	**#780**	**Adult Female**	**16/3/93**	**#742**
SL1	**Adult Male**	**10/5/89**	**#664**	**Adult Female**	**20/11/90**	**#665**
	Infant (Still-born)	15/1/94	#966	Infant (Still-born)	15/1/94	#967
SL2	**Adult Male**	**10/2/91**	**#656**	**Adult Female**	**30/11/91**	**#657**
	Infant (Still-born)	23/7/94	#970	Infant (Still-born)	23/7/94	#971
	Infant(Still-born ?)	6/1/95	-	Infant(Still-born ?)	6/1/95	-
SL3	**Adult Male**	**20/5/90**	**#869**	**Adult Female**	**28/5/90**	**#868**
	Adult Male	**1/1/93**	**#872**	(male changed 1/4/94)		
SL4	**Adult Male**	**1/5/91**	**#874**	**Adult Female**	**22/6/92**	**#888**
SL5	**Adult Male**	**9/6/83**	**#871**	**Adult Female**	**11/10/85**	**#870**
	Son	1/11/90	#876	Son	1/11/90	#877
	Daughter	1/5/91	#875			
	Infant (Still-born)	9/6/93				
	Infant	11/1/94	#968	Infant	11/1/94	#969
SL6	**Adult Male**	**1/5/91**	**#875**	**Adult Female**	**22/6/92**	**#889**

SL = *S. labiatus*, SF = *S. fuscicollis*, # = Zoo Record Number.

Table 3.E : Attempts to create mixed-species groups of tamarins.

GP1 : SL1 & SF1 : mixed together 22/9/92, failed due to aggression by the *S. fuscicollis.*

GP2 : SL1 & SF2 : mixed together 3/10/92, succeeded for period until 9/5/93, when the female *S. fuscicollis* died during labour. No other suitable female was available, and group was split.

GP3 : SL1 & SF3 : mixed together from 21/6/93 until 1/5/94, were separated for monospecific trials until 4/7/94, and then have been together since 5/7/94.

GP4 : SL2 & SF5 : mixed together from 12/11/93 until 12/4/94, were separated for monospecific trials until 9/7/94, and then have been mixed together since 9/7/94. One infant *S.fuscicollis* was reared in this group.

GP5 : SL4 & SF4 : mixed together from 12/11/93 until 7/1/94, when the male died, and the female subsequently died. Post mortem indicated signs of aggression on male, but not clear if this was inra- or inter-specific, as no cases of aggression were observed.

GP6 : SL4 & SF8 : mixed together from 5/7/94, and they have been together amicably since 5/7/94.

GP7 : SL3 & SF6 : mixed together from 5/7/94, and they have also been together amicably since 5/7/94.

GP8 : SL6 & SF2 : mixed together from 7/7/94, and they have remained a mixed group since this date.

3.7.2 Age categories.

Assigning all the individuals to age categories was not of paramount importance to the present study, as age was not a factor used for analysis, but it is noted that age of subjects may influence results (e.g. Cleveland & Snowdon, 1984). Nevertheless, it was only used as a criterion for deciding what developmental state an animal was in, so this could be compared in general terms, to see if this was a factor in any patterns of behaviour.

Previous studies of tamarins have used different criteria, depending upon species and researcher (see Neyman, 1978,1980; Cleveland & Snowdon, 1984; Price,1990a; Yamamoto, 1993; etc), but it has usually been based roughly around the inter-birth interval and age of sexual maturity. The inter-birth interval (IBI) of wild and captive individuals are reported to be different (Wolfe *et al.*, 1975), and in *S. fuscicollis*, for example, the average captive IBI is approximately 220 -250 days (Snowdon & Soini,1988), while wild populations may only breed once a year (Goldizen *et al.*, 1988). The position of captive *S. labiatus* is similar, with an average IBI of around 165 days (Ogden & Woolfe,1979), and again probably a yearly birth interval (see Chapter 2) Age of sexual maturity is not clear either , but for *S. fuscicollis* in captivity, it can be as early as 1 year or less (Epple & Katz,1980). Due to this, Goldizen & Terborgh (1989) suggest that sexual maturity in wild *S. fuscicollis* can be assumed to be at 1.5 - 2 years. A lack of equivalent data on *S. labiatus* necessitates that the *S.fuscicollis* data on sexual maturity be used. Both species, could be assumed to have a similar IBI, and so the following age categories were used;

Infant	0-6	months (based on minimal IBI).
Juvenile	6 - 12	months (based on 'year' IBI in wild).
Sub-adult	12-18	months (age until possible sexual maturity).
Adult	18 +	months (sexual maturity).

3.7.3 Records.

Details of all individuals at the Zoo were stored as computer records in the ARKS management and record programs. This allowed individual records of events such as births and deaths, dates of pairings, to be held. In addition, at the "old marmoset house" , a daily journal was kept of any unusual / interesting happenings concerning the animals (e.g. when animals were aggressive or mating). These data bases provided an accurate record of events concerning each of the study groups, even when I was not present at the Zoo.

3.7.4 Housing & husbandry.

As detailed earlier, there was a new enclosure built around the two end cages of the 'old marmoset' compound. These cages can be described as a "traditional" indoor /outdoor marmoset enclosure, similar to many other zoos (e.g. Mallinson, 1975). At the left side of the complex, there were 10 different indoor/outdoor cages (Numbered C1-C10), and on the right side there were an additional 8 (Numbered C11-C18 ; See Figure 3.E). The left side cages consisted of an indoor area of approximately 1.65 x 1.55 x 1.5m, furnished with a woodchip covered concrete floor, a shelf to rest and sleep upon and a heat-lamp to warm it, and also a 1.9 x 1.55 x 3.7m outdoor, mesh covered area, furnished with a few (on average 9) small, medium and large sized branches (Plate 4). The floor of the area was covered with bark chips, and had a 70cm concrete access strip running along the front of it. All indoor areas contained one or more plywood nest boxes, of approximate size 30 x 25 x 25cm, hung on the walls or placed on the large shelf (Plate 5). Branches were placed between the access hatch and the floor, to facilitate easy movement to and from the floor. The inside areas were thoroughly cleaned each day, and new wood shavings were put on the floor. Access between the adjacent cages was through doors which are shown in Figure 3.E. The front of each cage consisted of a 0.5cm thick perspex sheet, and this allowed clear vision of the animals. Adjacent outdoor cages, were separated by means of a double set of mesh, separated by a 3 cm gap between them, effectively stopping monkeys in adjacent cages having any physical access.

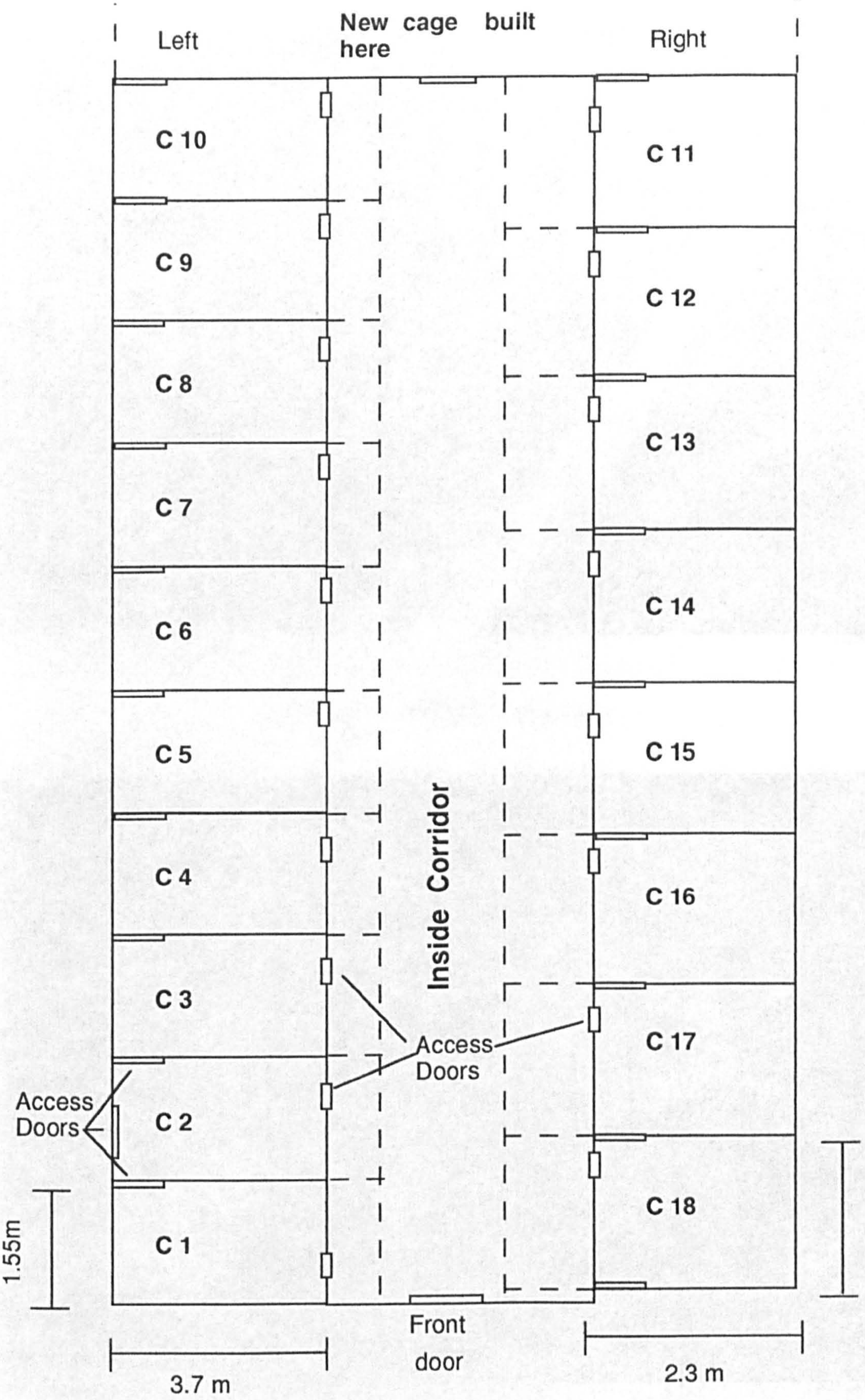


Figure 3.E : Schematic plan of the old marmoset house, not shown to scale.

Plate 4 : An Example of tamarin outdoor area.

Plate 5: Typical indoor area for tamarins at Belfast.

Visual access and olfactory contact could occur through the cages. The right hand cages had a larger (2 x 1.75 x 1.5m) similarly furnished indoor area but a smaller outdoor area (1.9 x 1.8 x 2.3 m) again containing a few branches (approx. 12) and a woodchip covered floor (Plates 4 & 5). Once again, there was a physical separation of adjacent groups. As mentioned in Section 1, tamarins were housed beside other Callitrichid species, as well as several bird species.

Table 3.F shows where the single species groups of subjects used in this study were housed. Groups of the same species were not housed directly beside each other. However, groups of both *S. labiatus* and *S. fuscicollis*, were housed beside each other before they were mixed together. Eventually, five mixed-species groups were formed (Table 3.E), and all other single species groups of *S. labiatus* and *S. fuscicollis*, were moved elsewhere. This left five mixed-species groups, and they were as follows; mixed group 3 (GP3 : SL1 & SF3 ; Housed in C9 & C10), mixed group 4 (GP4 : SL2 & SF5 ; Housed in C11& C12), mixed group 6 (GP6 : SL4 & SF5 : Housed in C5 & C6), mixed species group 7 (GP7 :SL3 & SF6 : Housed in C1 & C2), and mixed species group 8 (GP8 : SL6 & SF2 : Housed in C17 & C18).

Table 3.F : Original housing arrangements of single species tamarin groups, in the "old marmoset house", Belfast.

S. labiatus	SL1	C10	*S. fuscicollis*	SF1	C2
	SL2	C12		SF2	C17
	SL3	C4		SF3	C9
	SL4	C8		SF4	C7
	SL5	C1		SF5	C11
	SL6	C18		SF6	C5
				SF7	C13
				SF8	C15

All indoor areas were thermostatically controlled, and had a heatlamp and a heater under each bench, keeping the temperature at around 20-25°C, even during the winter. Lighting was mainly provided by artificial fluorescent strips, between 0800 and 1600 hours, and natural light entered through the access hatches between the indoor and outdoor areas. Animals were allowed free-access between indoors and outdoors, except for routine husbandry and for certain parts of the present study. Freshly prepared fruit, primate pellets, marmoset jelly, eggs, vegetables, chicken and occasionally insects (mealworms, crickets etc.) were given once daily (usually before 1230h). Food was mainly fruit and vegetables, and the protein element (e.g. eggs, chicken, marmoset jelly, insects) was varied over each week. Food was placed on the floor, or on top of the shelf. Vitamin supplements were given on a regular basis (generally multivitamins). Finally, fresh water was provided daily and was placed in a bowl in the inside areas.

3.7.5 Behavioural categories.

The behavioural repertoire of various species of tamarins can be described in a number of distinct ways, and has been categorised by several authors (e.g. Coates & Poole,1983 ; Snowdon & Soini, 1988; Garber,1980b; Price,1990a). However, no agreed ethogram of behaviour exists, and while each set of definitions are globally similar, they have been adapted to suit the needs of each researcher. Hence, in the present study, previously used definitions were adopted where appropriate, otherwise definitions were formulated to suit the purposes of each experiment.

Table 3.G : Mutually exclusive behavioural categories used to define activity of tamarins.

Behaviour	Definition
Look	Animals is in a stationary position, with scanning head movements (in both vertical and horizontal planes), or fixation of stare on object or animal may be divided into look up and look down.
Forage	Animal searches, by manipulating substrates or by visual inspection, through the area in an attempt to explore the area and/or gain an insect or plant food item.
Eat	Consume any type of food item.
Rest	Stay still and relaxed in any posture (does not include any other categories, e.g. groom, huddle etc.).
Huddle	Stationary contact with another, where torso and/or limbs are touching (does not include any other behaviour).
Groom	Individual picks through hair of another, with visual inspection and parting of the hair by hand(s) or mouth, or self grooms.
Play	Racing and acrobatic movements chasing or being chased, wrestling, rough-and-tumble and "mock" biting.
Locomotion	All movements (except play) in which the body is displaced relative to its surroundings (Garber, 1980b).
Alarm call	Animal calls out and acts in an alarmed manner, different from other behaviours, giving characteristic vocalisations (see Snowdon & Soini, 1988 for descriptions of vocalisations).
Scent Mark	The animal performs an act of depositing sent and /or urine upon a substrate divided into 3 categories; **Anogenital** ; in sitting position and rubs anogenital region back & forth and/or from side to side often leaves drops of urine, **Suprapubic** ; while lying on the abdominal region the body is pulled forward with the arms and the suprapubic region is rubbed over the substrate. **Sternal** sternal region is rubbed along the substrate.
Sexual Behaviour	Animal performs sexual activity. **Solicitation** ; female head-hakes and tongue-flicks in a pre-copulatory context (Price, 1990a. **Tongue flicks** ; rapid rhythmic protrusion and retraction of tongue (Snowdon & Soini, 1988). **Copulation** ; male mounts female, grasps her around the waist and leaning weight on her, thrusts back & forward (Price, 1990a)
Call	Utter any type of vocalisation other than alarm calls, e.g. long calls.
Other	Any behavioural pattern not otherwise listed (e.g. copulations, nursing infants, etc).

Table 3.H : Mutually exclusive categories of positional behaviour, used for tamarins (mainly based on Garber, 1980a,b; 1991).

Position	**Definition**
Sit	Squat upright with hind limbs or all four limbs resting on the substrate.
Quadrupedal Walk	Move forward with alternating movements of limbs with the contralateral fore and hind limbs more or less simultaneously making contact with the substrate, a Lateral sequence (based on Coates & Poole, 1983).
Quadrupedal Run	As quadrupedal walk, but using a faster gait.
Ascend	Move diagonally or vertically to a higher position than starting point. Separated from Quadrupedal Walk by the animal using a prehensile hold on substrate
Descend	Move diagonally or vertically to a lower position than starting point, either head first or tail first. Again separated from Quadrupedal Walk by the monkey gripping substrate with its limbs .
Bipedal Suspend.	Hang supported by fore- or Hind-limbs, with hands or feet gripping the substrate (Garber, 1980a).
Quadrupedal Suspend	Hang supported by all four limbs, with hands and feet gripping prehensively. This includes suspension by three limbs while manipulating an object. In this position the animal grasps the substrate and does not maintain weight by means of its claws (Garber, 1980a).
Leap	As colloquial use, e.g. jump.
Lie	Recline on substrate, either on back, front or side, with no weight on limbs.
Vertical cling & Leaping	A form of locomotion between large vertically orientated substrates, involves quadrupedal suspension, and leaping between the supports (Kinzey *et al.*, 1975).
Bound	Form of travel , characterised by a brief in-air phase of stride. Includes both asymmetrical and symmetrical hindlimb dominated gaits.
Stand	Upright stance using all 4 limbs, with body mass raised off the substrate.
Vertical Cling	Posture whereby the animals weight is borne by means of its tegulae (claws) on large vertically orientated substrates (Kinzey *et al.*, 1975).
Other	Any other position.

3.7.6 Activity.

The behavioural categories used with these captive tamarins were essentially the same as those used for the study of wild tamarins (see Chapter 2), but had to be reformulated in respect to the captive environment (Table 3.G). All these behavioural categories were used to describe the broad activity pattern of any animal, at any time, and encompassed all behaviours of interest in the present study. Each category was adapted from various sources (e.g. scent-marking was based on descriptions from Price,1990a; Snowdon & Soini,1988; and Coates & Poole,1983), to give an adequate definition to suit the two species being studied.

3.7.7 Posture and position.

Most of the literature regarding the posture / position of tamarins is based on the work of Garber (1980a,b,1984b,1991), and where appropriate the definitions used followed his descriptions. Table 3.H shows the definitions used for all parts of this study. These particular definitions had been used successfully in a captive study of *Leontopithecus rosalia* (Hardie, unpublished data) and were also found to be adequate for description of the positional behaviour of *S. labiatus* and *S. fuscicollis* in Bolivia (Chapter 2).

3.7.8 Substrates.

All substrates used by the tamarins were categorised on 2 complementary measures, size and orientation, regardless of their nature (i.e. whether or not the were natural or human-made, etc.). This was done once again in a manner identical to the methods used for Chapter 2, where the angle and size of substrate was estimated and placed into the following categories, Again based on Garber (1980a) ;

Angle of substrate used : **Horizontal** = 0-15°
Oblique = 16-74°
Vertical = 75-90°

(where all angles were measured as deviations from the Horizontal axis)

Size of Substrate Used **Small** <5cm
Medium 5-10cm
Large 10cm+

(where size was estimated diameter of substrate)

The captive environment produced some anomalies, due to the non-natural additions of mesh, concrete and cut wood. The following conventions were maintained, all floor areas were assumed to be large substrates, as was the roof and walls. The mesh was more problematic, as it was small units (e.g. links, grids etc.) but all joined together into a larger unit. The mesh was therefore regarded as a large substrate, but the postures used on this were different to those used on other large substrates, and this was noted.

3.7.9 Spatial relations.

Any measure of distances between subjects in the present study was made by estimation of distance. Before any data were collected, extensive practice of estimating distance was carried out, and was compared with known distances in the enclosures. Practice continued until estimates were accurate and were checked at regular intervals during the study, to ensure consistency. Distances used varied with each experiment and in all experimental conditions, distance estimation was practised prior to data collection.

3.7.10 Interactions.

For both species, there was the opportunity to interact with the other associating species, and this could be divided into two broad categories; aggressive and affiliative (friendly). Definitions were as follows;

Aggression ; included 6 main classes of behavioural interaction, which were mainly based on the work of Coates & Poole (1983) and Buchanan-Smith (1989), and most of which include "bared teeth squeals" (Coates & Poole,1983). The specific classes were as follows ;

Cuff : Hand is used swiftly to hit another individual

Headshake : The head is moved rapidly from side to side

Bite : as commonly used, is often directed towards face and neck region of individual and sometimes results in wounds.

Open Mouth Lunge : The head and mouth are thrust forward toward another individual, while the mouth is open sufficiently to reveal the lower canines.

Chase : Individual pursues another while attempting to make aggressive physical contact with them.

Fight : The individuals engaged in the aggressive interaction would interlock and bite and scratch each other.

All these behaviours can be termed as aggressive behaviour between individuals, and where possible the identity of both participants was noted. Other behaviours which involved dominance, but not necessarily aggression, include **food steal**, where one individual obtained food despite resistance from the possessor (Price, 1990a), and **displacement** where the direct approach of one individual led to the withdrawal of another individual. Although these latter two behaviours are related to dominance, they are scored separately from aggressive behaviour.

Affiliative behaviours were exactly the same as those which occurred in single species groups, and were therefore defined as cases of Groom, Huddle and Play, and Sexual Behaviour that occurred inter-specifically. Once again any incident of these behaviours were scored ad libitum when they occurred, and the identity of both participants was also noted.

3.7.11 Other behavioural definitions.

All experimental chapters deal with the specific measures involved, and they are consequently described in detail there. Some common definitions occurred throughout all the experiments and conditions, and these include measures of distance, interaction and behaviour. Any behaviour that did not meet with the exact criteria set out above was scored as "other", in the appropriate category.

3.7.12 Observation protocol.

Groups were sampled only in their outdoor areas, unless otherwise stated and they were locked-out in visual isolation from their adjacent neighbours. Unless the subjects were out of sight, the observer remained seated, some 2.5 - 3.0 metres from the front of the enclosures. All animals were well habituated to my presence (but see Caine,1990). Few alarm calls were ever given towards me, and it was assumed all groups behaved similarly to my presence.

3.7.13 Data collection.

All data were collected on purposely designed checksheets, and each one was tested prior to sampling. Checksheets were designed according to the recommendations of Hinde (1973) and Martin & Bateson (1986), and always included a column for noting any interesting/unusual observations. Time was denoted by a stopwatch, and sample intervals were noted by an electronic metronome, audible only to the observer.

3.7.14 Sampling methods.

In the present study, the large amount of potential subjects, and the frequent changes in activity, it was deemed infeasible to collect all occurrences of all behaviours. It was therefore necessary to adopt some type of sampling strategy.

A number of different sampling methods was employed, depending on the experimental design and the categories of behaviour to be recorded. For example, when detailed data were collected on each individual (e.g. Chapter 4), focal animal sampling (Altmann,1974) was used, but when the number of individuals performing a behaviour was the measurement (e.g. experiment 5.2, 6.1, 6.2), scan samples were appropriate (Martin & Bateson,1986). In other experiments, the identity of the individual that first completed the task was not of interest (i.e. experiments 5.1, 6.2, 6.3), but the duration to complete it was. Therefore, sampling strategy was varied according to the needs of the individual experiments.

Scoring of behaviour varied according to the nature of the experiment and for each measure was either 'all occurrence' sampling or 'instantaneous' sampling. Some experiments involved a mixture of both types of sampling rule ; for example, all occurrences of inter-specific interactions were noted in all experiments. Other measures were noted only when they were completed; for example in Experiment 5.1, the initial approach and touch were recorded. Most behaviours were sampled by instantaneous sampling, whether this was carried out on focal or scan samples (see Martin & Bateson, 1986 ; for a discussion of sampling rules).

Sample intervals were varied according to the nature of the investigation being conducted, and were as little as 15 seconds (experiment 5.1) or as long as 1 minute (chapter 4). Sample intervals were chosen on 2 criteria; firstly, was the sample interval of sufficient duration for the observer to note all appropriate behaviour, and secondly the chosen interval was based on those used in previous studies, provided that the first criterion was met (if not the interval was lengthened accordingly). The 15 second interval was only used in the one experiment, where a very limited amount of data was recorded, and had been used in a previous study of tamarin behaviour (Price,1990a).

Several studies have shown daily temporal patterns in behaviours such as activity and rest (e.g. Neyman, 1978; Garber,1980a; Pook & Pook,1982), which could potentially affect results. One way of controlling this, was to balance the observations between the groups, and between the time of day. All observation sessions were split equally between morning (0900-1230h) and afternoon (1330-1630h), unless stated otherwise

3.8 Reliability tests.

It is clear that any study needs to be an accurate representation of what the subjects are actually doing. This helps the study to have an external validity, and allows the experimenter to be sure that they are actually sampling the behaviours and categories that they assume to be. Following Martin & Bateson (1986), a form of checking the reliability of the recording methods used in the present study was conducted. Specifically, tests of inter-observer reliability were carried out for my own data collection techniques.

Table 3.I : Groups used and data type collected during inter-observer reliability trials.

Experiment / Chapter	Groups	No. of Samples	Type
Free-ranging, Ch. 4.	SL1,SF3	4 x 30 minutes	(a) Position (b) Activity (c) Substrate (d) Distances
Novel Objects, Ch. 5	SF1,SL5 SF4, SL4 SF5, SL2	12 sessions, (2 per group).	Duration ; a) *To exit* b) *To approach* c) *To touch`*
Food/Non-food, Ch. 5	SL5, SF2	2 x 15 min (food) 2 x 15 min (non)	(a) Duration to enter (b) No. Individuals in / on apparatus
Check Threats, Ch. 6	SL2, SL4	4 x 20 min	Duration a) *To each check* b) *Of checks*

3.8.1 Inter-observer reliability.

Assessments of inter-observer reliability were made for each main experimental type. Every one used the same single observer (R.Day), who had previous experience of observing tamarins, and who carried out some of the actual observations for Chapter 4. The behavioural and positional categories were practised extensively before the free-ranging study, and exact definitions of behaviour were finalised.

The behaviour of eight different groups (SL1,SL2,SL4,SL5, SF1,SF3, SF4,SF5) was observed simultaneously by myself and RD. For each type of behaviour being tested, at least two groups were studied, with a minimum of one of each species. These tests were run under the same conditions as when data were collected, using the standard checksheets. The exact details of tests and groups used, are given in Table 3.I.

As measures of reliability have to reflect the purpose for which the behaviour is recorded (Caro *et al.* ,1979; Martin & Bateson,1986), it was appropriate to use two measures of inter-observer reliability.

a) Correlation of reliability.

For the overall positional and behavioural data used mainly in Chapter 4, it was deemed appropriate to use a correlation method of reliability. This was because the overall proportion of time spent in each of the activity, behavioural, spatial and positional categories were the important factors. Analysis was to be at the level of comparing mean scores between the species and /or conditions, so exact concordance was not essential, only an overall agreement between observers on the proportion of time spent in each category. Following the procedure outlined by Martin & Bateson (1986), it was appropriate to set a correlation of 0.7, as being the minimal acceptable value. A Pearsons correlation (r) was calculated between the scores of the two observers for positional and activity categories, and also for spatial measures.

Table 3.J : Inter-observer reliability of categorical, distance and spatial relationship measurements (based on 4 x 30 minute sample sessions, with 1 minute sample intervals).

	Pearsons r (N = 120)	Mean Correlation
Distance & Spatial Measures:		
Height	0.94	
Distance from base	0.97	
Distance to own species	0.85	
Distance to other species	0.95	**0.93**
Categorical Measures :		
Activity	0.78	
Position	0.69	
Orientation of substrate	0.96	
Substrate size	0.70	
Location of subject	0.92	**0.81**

b) Index of concordance.

For all the other experiments, the main sampling method was usually time or exact occurrence based, and the important factor was an exact agreement between the observers over when and where the behaviour happened.

For these experiments, the time for events to be completed, and the individual number of occurrences were important. Also, in experiment 6.3, the total number of checks and duration of checks were compared, as frequency and duration were the variables being studied. The formula used follows Caro *et al.* (1979). Agreements and disagreements on each occurrence were scored, and reliability calculated using the formula A/(A+D), where A is the number of agreements, and D the number of disagreements. An observation was only recorded as an agreement, if the observers recorded the event as occurring within 2 seconds of each other, otherwise it was classed as a disagreement.

The scores of each observer were calculated for each behaviour and for each test session separately, and measures of reliability were calculated. Mean coefficients of reliability were then obtained for each behavioural and experimental category.

The results of the tests are presented in tables and 3.J (Pearsons correlation) and 3.K (Index of concordance). Overall, reliability was considered to be an acceptable standard for all behaviours. Although reliability for activity, positional and substrate (i.e. categorical) sampling was slightly less than for spatial and distance measures, this was not considered to be a major problem, as almost all individual measures were over the minimally accepted level (i.e. correlation of 0.7, Martin & Bateson, 1986). Only the position category was found to be less than this, and that was only marginally under the acceptable level (0.69). So it was concluded that the inter-observer reliability was of sufficiently high standard for me to be confident of the accurate measurement of my behavioural categories. All durations were very similar for both observers, and all concordances were at the 90% level or above, thus showing accurate measurement of durations.

Table 3.K : Inter-observer reliability between two observers, of experimental categories, calculated as an index of concordance (compared per species, and overall).

Experiment	Species[1]	Total No.	Agreements	Disagreements	Index[2]
Novel objects[3]	SF	18	16	2	0.89
	SL	18	17	1	0.95
	Both				**0.92**
Food/Non Food objects.	SF	79	78	1	0.99
	SL	78	76	2	0.97
	Both				**0.98**

No. of Checks of Threatening Stimuli.	SF	13	13	0	1.00
	SL	29	26	3	0.90
	Both				**0.95**
Duration of Checks of Threats[3]	SF	13	11	2	0.85
	SL	29	25	4	0.86
	Both				**0.86**

1. Both species are compared separately, and then the combined score is presented.
2. Index of reliability calculated from the formula A/(A+D), where A (agreements) = the lower of the two scores obtained by the two observers, and D (number of disagreements) = the number of differences between the two measures
3. Calculated as an agreement, if the events are scored as happening within 2 seconds of each other.

3.9 Analysis of data.

Most data were analysed on a 'by experiment', single species or mixed-species basis. Mean scores per session, or per object, were calculated for each category of interest and used in subsequent analysis. Such means were considered independent samples for statistical purposes.

The use of statistical tests followed Castellan & Siegel (1988), Coolican (1990) and Greene & D'Oliveira (1982). The small sample sizes used in most of the studies' experiments, meant that normality of data could not be expected, and parametric statistical tests were not appropriate. Instead, non-parametric tests were used. Significance was usually set at $p = 0.05$, regardless of whether one or two-tailed tests were used. Two-tailed tests were used unless direction of effect was predicted, whereby a one-tailed test was appropriate.

Data were analysed on an Apple Macintosh Classic II computer, using the statistical packages STATVIEW 512+™ (Abacus Concepts, 1988) and STATWORKS™ (Cricket Software, 1985).

Chapter 4 : A Comparison of the Behaviour in Captive and Wild Mixed-Species *Saguinus* Groups.

4.0 Introduction.

In order to determine whether or not the costs and benefits of association that are suggested by experiments on captive mixed-species groups, could be equated with those of their counterparts in the wild, it is first necessary to show that these two conditions are sufficiently comparable. This type of evaluation is conducted in order to determine if the findings of the captive research program have a high degree of ecological validity, meaning that the behaviour in both captive and wild situations can be compared in some empirical way. The most important factors in tamarin mixed-species are related to the relationship between the species, as these are measures which do not rely completely on ecological factors found only in nature, but are parameters which are essential to describe the spatial patterns between the species. Specifically, these are measures such as the direction of dominance, vertical partitioning within the environment and the spatial distance between the species. These parameters are compared and contrasted in 2 separate conditions;

a) five mixed-species groups in the large "new enclosure", and
b) one mixed-species group free-ranging over a small wooded area.

4.1 Tamarin mixed-species groups.

In a natural environment, mixed-species groups may be defined as the association between species which is shown to have a non-random coincidence in time and space, (see Chapter 1). Definitions of association may be different for different researchers (e.g. < 20m, Heymann,1990b; <50m, Buchanan-Smith, 1989), but one which compares average intraspecific and interspecific distances, may provide a useful criterion for determining if an association is taking place (e.g. Whitesides, 1989).

When in association, the species appear to have few interactions, and appear to tolerate or virtually ignore the others, at least in terms of direct contact (both affiliative and aggressive), and where this does occur, it is usually aggressive (Terborgh,1983; Norconk,1990b; Heymann, 1990b; Pook & Pook,1982; pers. obs.). The species have a vertical segregation in terms of height of forest utilised (see Chapter 2) and are often found at different heights at any point in time, except during fruit feeding where they overlap extensively in terms of fruit species consumed (Terborgh,1983; Garber, 1993b; Buchanan-Smith,1989; Chapter 3). This suggests that the vertical partition of tamarins during most activities allows little opportunity (or indeed need) for physical contact in natural conditions and so this would account for the paucity of interaction except where the conditions "drive" them to interact in a competitive manner.

In mixed-species *Saguinus* groups, the congener has priority of access over the *S. fuscicollis* and can displace them from a desired area (e.g. Terborgh, 1983; Buchanan-Smith, 1989; Chapter 2). This is normally shown in terms of the more dominant species displacing the other species or individual from the desired area without direct physical contact, although more rarely physical aggression will occur (Norconk,1990b; Heymann, 1990b). Most of these interactions appear at areas of restricted food resources and these are often small crowned feeding trees (Heymann, 1990b; Terborgh, 1983). Peres (1991) has demonstrated that *S. mystax* were generally first to enter large and medium sized feeding trees, where food was superabundant, and the *S. fuscicollis* tended to only feed after their congeners. These trees were also found to be tall, and mainly found in the canopy (Peres, 1993b), and this is the area of the forest where members of the *S. mystax* group are found (see Chapter 1). The *S. fuscicollis* are usually found at a lower mean height (e.g. Norconk, 1990b; Pook & Pook, 1982; Terborgh,1983), and were shown to be first to find most small, monopolisable resources, which were found in the lower canopy area (Peres, 1991). However, in general the *S. mystax* quickly displaced their congeners and took the resource (Peres, 1991). In all types of interactions, the *S. labiatus* have priority and are able to demonstrate this dominance, in terms of displacements and shows of aggression.

The purpose of the present study is to compare the vertical partitioning of captive mixed-species tamarin groups, to examine the intratroop spatial dynamics, in terms of within and between species distance, and to see if the two species generally behave in a manner which can be related in broad terms to the behaviour of their counterparts in the wild.

Section 4.A : Spacing, height use and interactions in 5 captive mixed-species groups.

4.2 Introduction.

In a captive situation, there is usually an abundance of food provided, and therefore it is not a limiting factor as it may be in the natural conditions. The small size of captive enclosures also produces another factor not usually present, namely the constant coincidence in time and space between the species due to their confinement. This would allow an increase in the amount of time the species would be in close contact, and would presumably allow for an increased opportunity for the species to interact with each other. Coupling this with the presumed decreased amount of competition between the species, may allow for more affiliative interaction between them than in the wild state. This was shown to be the case in a captive wild caught group of *S. fuscicollis* and *S. mystax* in Peru. There was a some social interaction between the species, with the patterns being "essentially the same as in intraspecific contexts", and in particular interspecific grooming was fairly common (Heymann & Sicchar Valdez, 1988). Interestingly, only *S. mystax* acted as groomers, and this may be linked to their dominance over *S. fuscicollis*.

In the present study the spatial relations between the species was compared, in terms of close contact, both between and within each species. This was in order to compare the association in terms of whether it could be described as an association between 2 pairs of 2 species, or as a single group of 4 animals. In effect, it was a comparison of whether or not the intraspecific close contact was more common than the interspecific close contact. It was thought that the 2 species would be in closer contact with their own species than with the associating species, so it was predicted that the amount of close contact (defined as within 1m of focal subject) would be greater intraspecifically than interspecifically.

The main predictions were ;

(1) That *S. labiatus* would have a higher mean height.

(2) *S. labiatus* would be more dominant

(3) Both species would spend more time in close contact with their own species, than with their congeners.

4.3 Methods.

During the summers of 1993 and 1994, five mixed-species groups (GP3, GP4, GP6, GP7 & GP8) were each studied for a period of approximately 1-2 weeks. They were placed in cage C10, and allowed access to the large end enclosure of the "old marmoset" house (see Figure 3.A). After an initial period, once the species had become habituated to their surroundings, their behaviour was recorded. All individuals were observed for 8 x 15 minute sample sessions, divided equally between morning (0900-1230h) and afternoon (1300-1630h), with each individual being treated as a focal subject (Martin & Bateson, 1986) all receiving the same number of sessions. All sample intervals were 20 seconds and this resulted in 45 sample points for each session. All subjects received 1 hour (i.e. 4 sessions) in the morning and 1 hour in the afternoon. Observations were infrequent due to cold and wet weather throughout the period of the study.

The following behaviour was sampled instantaneously at 20 second intervals.

i) Height of focal animal

ii) Area of enclosure (as in Chapter 3).

iii) Distance to same species (Contact,<15cm, 15-50cm, 50cm-1m, 1m+)

iv) Distance and identity of other species if less than 1m from focal individual (categories as iii).

Each sample session was conducted at least 10 minutes after another session and no two adjacent sample sessions were conducted on the same individual. Observations were only carried out when the weather was dry and mild. All behavioural categories that involved the estimation of distances and/or heights were practised until the observer could accurately assign observations into the appropriate height or size class. In addition, heights were marked on the cage frame to assist accuracy.

As well as the above data, all interactions between the species (no matter what individuals were involved) were noted ad libitum. These included all events, both aggressive (e.g. chases, head shakes, fighting, etc.), affiliative (e.g. grooming, huddling, resting together, etc.), or any other type of interaction. Behaviours were placed into specific categories (as defined in Section 3.7.10), and the following data was collected on each incident ;

a) Context (i.e. aggressive, affiliative or other)

b) Individuals involved

c) Exact form of interaction

d) Reaction of individuals (i.e. who fled, was aggressive etc)

e) Area of cage

4.4 Results.

Figure 4.A shows that there was a significant height difference found between the species ($U=0$, $N_a=10$, $N_b=10$, $p<0.01$), where the mean height used by the *S. labiatus* (1.98m, St. error 0.1) was greater than that of *S. fuscicollis* (1.43m, St. error 0.1). However, the range of heights used was similar, where both species used all areas, from the floor upwards. In both species, the sexes did not significantly differ in mean height use (*S. labiatus* ; $T=11$,$N=5$, *S. fuscicollis* $T=9$, $N=5$, both non-significant).

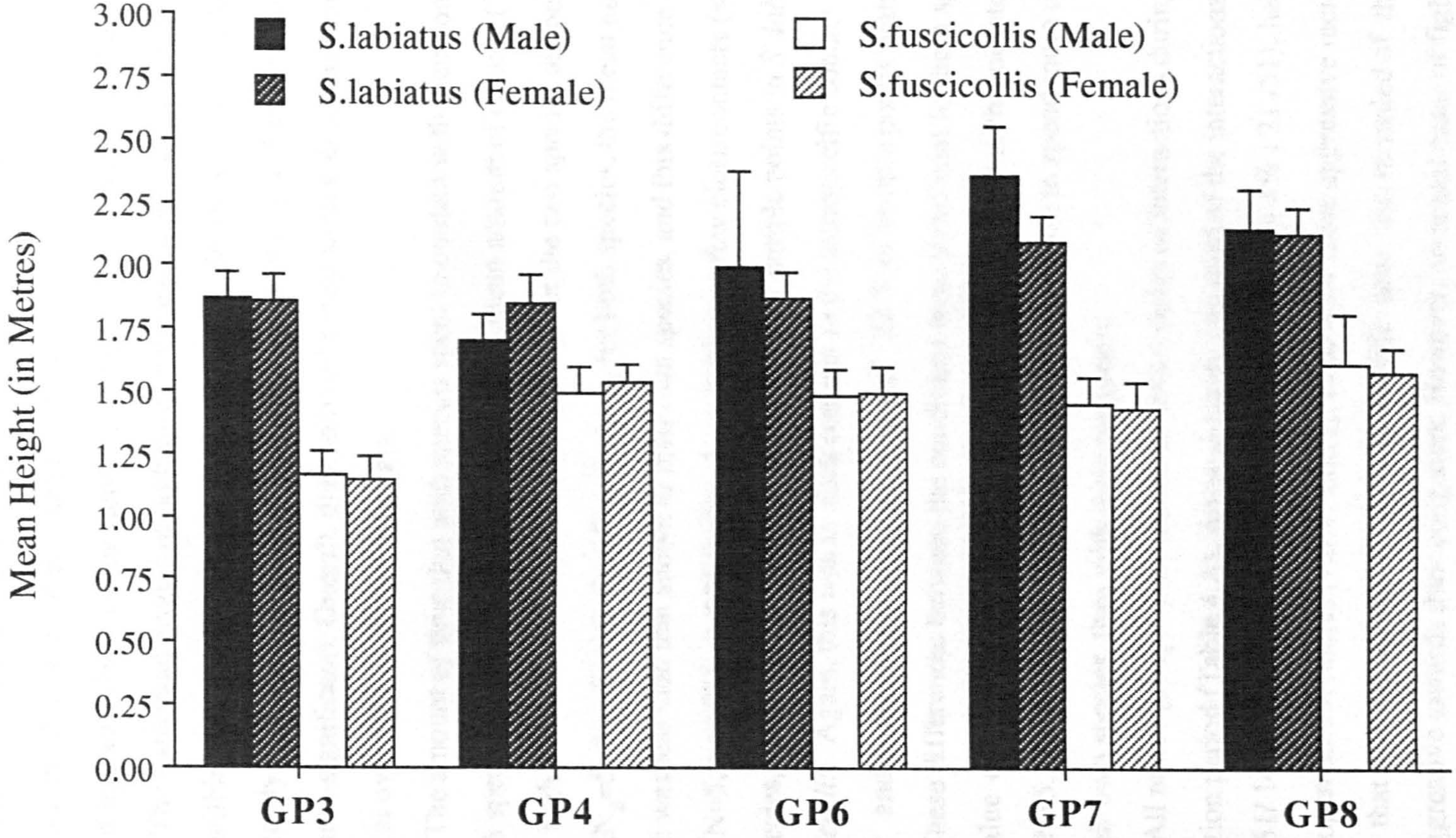


Figure 4.A : Mean height used by groups of each species, during mixed-species trials. Bars show standard errors.

Also, it is important to note that both *S. labiatus* individuals in each mixed group were found at a higher mean height than their congeners (Figure 4.A). One species difference that contributed to the overall pattern, was that the *S. fuscicollis* spent significantly more sample periods on the floor area of the cage ($U = 6$, $N_a = 10$, $N_b = 10$, $p < 0.01$), having approximately 4.3 % of intervals down on the floor, compared to the 0.2% of *S. labiatus.*

The individual groups of both species were shown to spend at least 43% of sample points within 1m of their own species (Figure 4.B). So, the two species did not differ significantly in the amount of time they spent close (<1m) to their own species ($U = 12, N_a = 5$, $N_b = 5$, non-significant). Overall, they both had a very similar mean percentage of time in close contact at over 50% of sample intervals.

The amount of time that both species spent in contact with their congeners, was similar for both species (Figure 4.B). *S. labiatus* had a mean amount of contact (30.9%) that was slightly higher than that of *S. fuscicollis* (28%), but the two species did not differ significantly ($U = 12, N_a = 5$, $N_b = 5$, non-significant). Also, for both species, the mean number of such contacts was less than that shown to their own species, and this difference was significant ($T = 15$, $N = 5$, $p < 0.05$). Additionally, there were very few close contacts (<50cm) between both species, and these accounted for only 5.4% of sample points in *S. labiatus* and 4.3% in *S. fuscicollis.* Again, this was in stark contrast to the intraspecific contact, where both the *S. labiatus* and *S. fuscicollis* spent in excess of 22 % of sample points within 50cm of each other. These differences between the conditions were significant for both species, where the mean value of intraspecific contact was significantly higher than that of interspecific contact ($T = 15$, $N = 5$, $p < 0.05$). Therefore both species were shown to spend more time in close contact with their own species, than with their congeners.

All mixed groups were shown to have a series of interactions during the course of the observation period (Table 4.A). Approximately one third of the interactions were aggressive (35% : 51/ 146), and these were split between, chases (14.4% : 21 /51), head-shakes (11% : 16/51), open mouth lunges (7.6%: 11/51). In most of these aggressive incidents, it was the *S. labiatus* that was the aggressor, and only a single case was recorded of the *S. fuscicollis* being aggressive towards their congeners. However, no actual cases of fighting were noted, and generally the species coexisted peacefully. Food stealing only accounted for a very small part of the results (2%: 3/51). More typical of interactions, was where one species was non-aggressively displaced from a desired spot, by the approach of another.

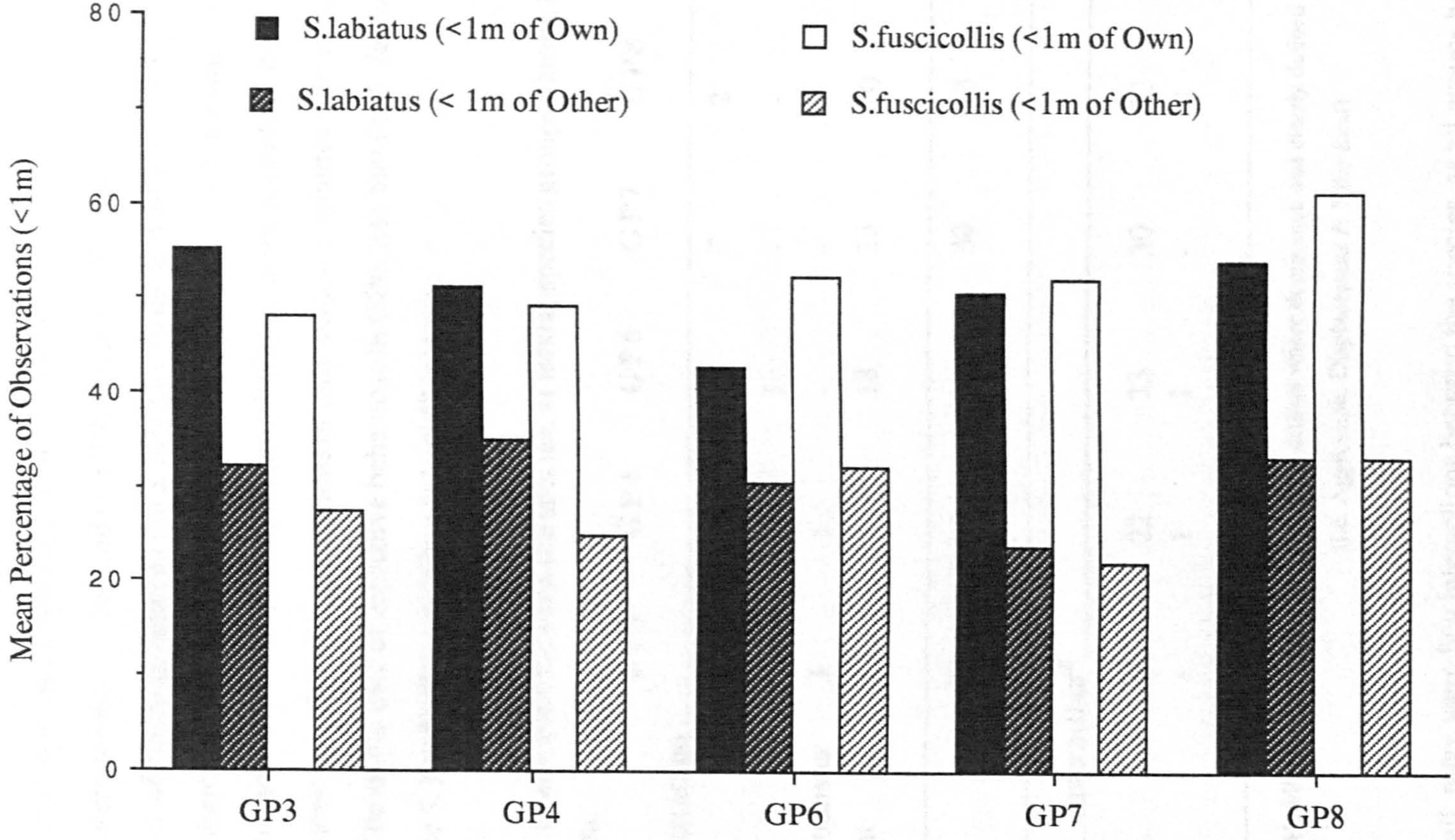


Figure 4.B : Mean percentage of observation points, where each individual was within 1 metre of their own species and their congeners.

Such displacements accounted for over one half of all interactions (56.2% : 82/ 146), and in the majority of cases (97.6% : 80 /82) , the *S. labiatus* displaced the *S. fuscicollis.* There were few other incidents between the species, except that there were 9 incidents of affiliative behaviour, and 2 food begs exhibited between the species (Table 4.A). These affiliative behaviours were strongly influenced by GP4, which had 8 of these incidents. These included one incidence of huddling between the *S. labiatus* male and the juvenile *S. fuscicollis* (< 10 second duration), a case of the *S. fuscicollis* male grooming the *S. labiatus* female, but were dominated by one or more of the *S. labiatus* playing with the juvenile *S. fuscicollis* (6 /8 cases). The total duration of these sessions of play exceed 5 minutes, and were non-aggressive in nature. The single case of affiliative behaviour in GP6, was that the *S. labiatus* male pulled the tail of the *S. fuscicollis* male in a "playful" manner.

Table 4.A : Interactions between the species, in mixed-species groups, during height and spacing trials.

	GP3	**GP4**	**GP6**	**GP7**	**GP8**	**Total**
Nature of Interaction						
Aggressive	10	18	14	7	2	**51**
Affiliative[1]	-	8	1	-	-	**9**
Food Begs/ transfer	3	1	-	-	-	**4**
Displacement	15	5	18	23	20	**82**
Total	27	32	34	30	23	**146**
Direction of Interaction[2]						
Lab. > fusc.	26	22	33	30	22	**133**
Fusc. > lab	-	1	1	-	1	**3**

[1] Huddle, Groom or Play. [2] Scores on actions where dominance was clearly defined (i.e. Aggression, Displacement & Take food)

Overall, there were few interactions between the species, as all groups had a mean number of interactions of less than 30, which means that on average, there were less than four between species interactions per hour. Aggression was found at a mean rate of 1.3 incidents per hour, indicating that the species did show an antagonistic existence, but lived together reasonably amicably. Males were the actors on 56.8% (83/146) of incidents, with 40.4%

(59/146) being carried out by females and the remainder being joint actions (4/146). Females were on the receiving end of 44.5% (65/146) of interactions, with males getting 42.5% (62/146), and the rest were shown towards both sexes jointly, or to the *S. fuscicollis* juvenile. Therefore there seems to be no sex differences in the way interactions occur.

4.5 Discussion.

In the wild, the associating species are found at a higher level of the forest than *S. fuscicollis,* (see Chapters 1 & 2). This was clearly shown during the present study, and an identical pattern was also found in a pilot study, where the first 2 groups that were tested as single species groups. It appears that the vertical partitioning shown by the tamarins while in mixed groups was not an artifact of being in the mixed groups. In all areas, whether they are found monospecifically or in associations, *S. fuscicollis* are found to utilise lower mean height areas of the forest, than the corresponding height used by members of the *S. mystax group* (e.g. Soini, 1987; Crandlemire-Sacco,1988, for monospecific groups of *S. fuscicollis* ; Terborgh, 1983, for mixed-species groups of *S. fuscicollis* & *S.imperator*; Norconk, 1990b, for mixed-species groups of *S. fuscicollis* & *S. mystax* and Yoneda, 1981,1984a for mixed-species groups of *S. fuscicollis* & *S. labiatus*). The cause of the vertical partitioning, (which presumably is a factor that alleviates competition between associating species ; see Chapter 1), appears to be an adaptation on the part of *S. fuscicollis* to utilise lower areas of the forest than other tamarin species, rather than being forced to do so by direct competition. This notion is further supported by the finding that *S. fuscicollis* are morphologically specialised for clinging to, and locomoting upon, the large vertically orientated supports that are found in the lower areas of the forest (Garber, 1991,1992). Finally, further support comes from the fact that a monospecific group of *S. fuscicollis* conducted the majority of their insect foraging, travelling and resting, at heights of 5 metres or less (Soini, 1987). This accounted for some 50% of all observations, and indicates a utilisation of this area in the absence of a congener.

Part of the height separation found in the current study, may be explained by the larger amount of time *S. fuscicollis* spent on the floor area. This pattern has been found in other mixed-species groups of tamarins (e.g. Heymann, pers comm., Norconk, 1990b; Peres, 1991), where individuals of both species go down to pick up fallen food items, and to capture insects, and these were also the main reasons for being on the floor in the current study. In addition, both *S. fuscicollis* and *S. labiatus* have been observed to cross open areas in the wild (e.g. roads, wide paths), where they descend to the ground, and proceed to run and or bound, quickly across the gap (pers. obs.). A similar tendency was found in the present captive groups, where both species occasionally used the ground to travel across the large enclosure.

In theoretical terms, in order to call a mixed-species group an association, it is necessary to show that the species have a coincidence in time and space, that exceeds the levels of mere "chance" encounters (Waser, 1982, 1984). However in the present captive study, the formulae used to determine association in the wild were not appropriate, as captive groups could not have appropriate measures such as population density, and mean daily path lengths. Also, the subjects themselves were in an enclosed area, and not able to move far away from their congeners, even if they desired to. However, there was some evidence of association, as both species spent over one quarter of observation time in close contact (<1m) with each other, even though they had the opportunity to keep apart. This suggests that they did indeed have some sort of relationship and did not avoid each other. Nevertheless, both species were found to have a much closer amount of contact with their own species, than with their congeners. This was a pattern that is typical in primate associations, where the nearest neighbour tends to be a conspecific rather than one of the associating species (e.g. Cords, 1987; Heymann, 1990b; Whitesides, 1989). This means that the captive groups were made up of two sub-groups of two species rather than a single unified group, and this was again similar to the way that mixed-species groups of tamarins behave in the wild (e.g. Buchanan-Smith, 1990a; Peres, 1991; Terborgh, 1983). In effect, this means that the current study compared the behaviour two species of tamarins that demonstrated tolerance of each other's presence.

In mixed-species groups of primates, there may be interactions between the various species involved (e.g. Abordo *et al.*, 1975; Peres, 1993a; Richard, 1970; Terborgh, 1983; Waser,1987), and these interactions may be affiliative (e.g. Peters & Nogge, 1986; Struhsaker, 1971) agonistic (e.g. Cords, 1987, 1990b), or the species may ignore each other. However, in mixed-species groups of tamarins, the actual rate of interaction is usually very low (e.g. Peres, 1991 Pook & Pook, 1982; Terborgh, 1983;Yoneda, 1981, 1984a), and may be as infrequent as 1 observed event for every 5 hours of observation (Heymann, 1990b). The current study had a relatively high rate of interaction, at approximately 4 incidents per hour, but these were mostly displacements, whose numbers may have been exaggerated by the confined space in captivity. Aggressive incidents were less common, and these mainly consisted of chases and head-shakes, where the larger-bodied *S. labiatus* was dominant over the smaller-bodied *S. fuscicollis.* The direction of dominance was as predicted, and corresponds with previous studies of mixed groups of these two species (Buchanan-Smith, 1990a; Garcia, pers. comm.; Pook & Pook, 1982; Yoneda, 1981), and in mixed-species groups of tamarins, where *S. fuscicollis* are dominated by their congeners (e.g. Peres, 1991; Terborgh, 1983). A similar pattern was also found in the other captive mixed-species groups of tamarins that have been formed elsewhere (Barathy, pers. comm.; Epple, pers. comm.; Heymann & Sicchar Valdez, 1988).

Affiliative interactions between the species occurred at a rate of around 1 interaction per 4.5 hours of observation. This rate was lower than that of the only comparable captive study (Heymann & Sicchar Valdez, 1988), but there was much variation over the course of that study, where no interspecific grooming was noted until after the species had been together for 5 months. Other studies of tamarin mixed-species groups in the wild, did not show any grooming, or other affiliative interactions between the species (Peres, 1991; Terborgh, 1983). However, interspecific affiliative behaviours such as grooming do occur in other mixed-species primate groupings (e.g. Gautier-Hion & Gautier, 1974; Mittermeier, 1973; Waser, 1980), and Heymann (1990b) has described three "play invitations" by one *S. fuscicollis* towards a *S. mystax*. There remains the possibility that some unrecorded affiliative interactions may occur between associating species, as the subjects in any field study are not in sight of the observer for the whole observation time. However, only detailed long term field studies will answer this question.

The range and type of interactions seen in the current study, when including all cases of interactions, show a similar range of interactions to those reported for other mixed groups (Heymann, 1990b; Peres, 1991). Comparing these interactions with intraspecific interactions (e.g. Heymann, 1990a; Heymann, in press) it appears that although the amount was less, the patterning of them was "essentially the same as in intraspecific contexts" (Heymann & Sicchar Valdez, 1988 : 223). There was also a developmental component to their study, where the level of interaction varied over time, and with the group composition and over the course of a pregnancy within the *S. fuscicollis* group. This suggests that the level of interaction may vary over time, for a number of possible reasons. In the present study, the largest number of affiliative interspecific interactions were between the two *S. labiatus* and the infant *S. fuscicollis* in group GP4. This is not surprising, as several other studies of primate polyspecific associations have indicated that juvenile or younger members of groups, are more likely than older individuals, to interact playfully with members of the associating species (e.g. Cords, 1987; Gartlan & Struhsaker, 1972; Klein & Klein, 1973; Oates & Whitesides, 1990).

However, it will remain to be seen if there is a similar pattern occurring in the present captive mixed-species groups of tamarins, as to date there has only been one successful birth in the groups.

4.6 Summary.

Captive mixed-species groups of tamarins, were found to exhibit a vertical separation, in terms of mean height used in their enclosures. In *S. labiatus,* all individuals used a higher mean height of the enclosure, than all the *S. fuscicollis* individuals. This pattern of separation was similar to that shown in wild groups. The mixed group was made up of two separate groups of different species, which spent more time closer to their conspecifics than to their congeners. However, both species spent over one quarter of their time within 1 metre of each other, indicating that the members of both species were not avoiding each other. There was a range of interactions shown between the species, where *S. labiatus* was clearly dominant, and the few friendly contacts exhibited, were concentrated between both the *S. labiatus* and a juvenile *S. fuscicollis.* Overall, the captive mixed-species tamarin groups were seen to behave similarly to their counterparts in the wild. The study demonstrated that these mixed species captive tamarin groups in an enclosed cage, had behaviour which was sufficiently comparable with that of their wild counterparts, in terms of vertical height used. However, the fact that both species were in an enclosed area may have been the only reason for the two species spending any time within 1m of each other, and the mixed-species groups may only be two monospecific groups tolerating each others' presence. In order to test this idea, a mixed-species group was allowed to free-range in a small wooded area (see below).

Section 4.B : The behaviour of a captive free-ranging mixed-species tamarin group.

4.7 Introduction.

In the mid-eighties an innovative approach was taken towards the exhibition and husbandry of captive golden-lion tamarins at the National Zoological Park, Washington. This involved allowing a family of 6 tamarins to roam freely in a quiet area of the zoo (Bronikowski *et al.*, 1989). This approach has been successful and has been applied to lemurs at Belfast Zoological Gardens (*Lemur catta* and *Lemur macaco* ; personal obs.) as well as to *Saguinus oedipus* at Jersey Wildlife Preservation Trust (e.g. Price *et al.*, 1989,1991). In all cases, the animals quickly became accustomed to their new areas and their behaviour became adapted to their new surroundings. The goal of free-ranging exhibits has often been to allow animals to adapt to more natural surroundings than those usually used in zoos (Bronikowski *et al.*, 1989) and can be a first step towards the "training" of captive born tamarins to be able to be released (e.g. *Leontopithecus rosalia,* Beck *et al.*, 1990). The main feature is that these captive animals are allowed a measure of freedom, while they are still within a larger enclosed area, and can receive veterinary help and be provisioned. Also they can learn to locomote on substrates not available in their normal enclosures, and may even become disorientated and get "lost" (see Price *et al.*, 1989; Beck *et al.*, 1990). If all this is learned in a "safe" (i.e. predator free environment) it is hoped that these individuals may cope better when released into a natural environment (Box,1991a).

4.8 The significance of a free-ranging mixed-species tamarin group.

The prospect of free-ranging tamarins, as well as being an attractive form of display, has important implications for mixed-species groups. In their natural habitat, mixed-species groups of tamarins occur throughout all areas of geographical overlap between *S. fuscicollis* and its congeners (see Chapter 1), and despite the fact that these mixed-species tamarin groups can be formed in captivity (see Chapter 3; Heymann & Sicchar Valdez,1988; Hardie *et al.*, 1993), there is a validity problem in terms of whether or not these situations are essentially the same. How do you decide whether a mixed-species group is forming an association or not ? Although different researchers have used different definitions for association (Chapters 1 & 2), the main agreement is that association can be defined as a coincidence in time and space that is not due to chance encounters alone (see Waser, 1980,1984). In a conventional captive situation, by necessity, the species have to share an area that is very small in size when compared to their natural range size. This gives a high level of the species sharing time and space, and indeed they can hardly not coincide even if they did not want to. Also, as previous researchers have used such large distances to denote "association", this clearly is not applicable in the current captive enclosures where they can only be around 10m apart at the very most.

This is where the free-ranging exhibit comes into its own. As the 2 species will be not constrained within a limited area, any relationship that occurs will be through some level of "choice" (as each has the potential space available to avoid each other) and not enforced, as in the enclosed areas. If the species show some sort of spatial cohesion, whereby both are close temporally and spatially, then one can conclude that these species really do associate in captivity. On the other hand, if the species do not associate in any clear and coherent way, it may suggest that the association is is not the same as in wild tamarins, and suggests that captive mixed-species groups are not forming associations, but are merely tolerating each others presence in a confined area. This is extremely important, as if the two species are not shown to associate then it is difficult to provide justification to the assumption that the behaviour of captive mixed-species groups in any way resembles those in the wild.

Another consequence for captive born animals being allowed to free range is that the experience can be described as improving their welfare. The main theoretical point is that in natural conditions the species have to deal with unpredictable environments, and this allows for flexibility in behaviour (see Box, 1991c). Therefore, an introduction to a large degree of novelty and unpredictability, as well as potential for danger, can be seen as being beneficial for animal welfare (Poole,1990,1991a,b; Redshaw & Mallinson,1991; Box, 1991a). For example, Beck (1991) argues that captive environments providing hidden food, and non-rigid substrates, could force tamarins to hang, climb, jump and move considerable distances.

The purpose of studying the free-ranging tamarin group was therefore to test some predictions and assumptions about the association produced in captivity. Also it could be used to examine the effects on substrate use and ranging when the two species are released as well as testing the activity budgets before and after release. The following predictions were tested :

1) If there is an association, it is predicted that the two species should show a greater than chance coincidence in time and space, i.e. they should spend time close to each other, and <u>not</u> avoid each other.

2) That the more dominant *S. labiatus* would displace the *S. fuscicollis* from desired objects or positions. This may include "novel" resources found initially by the *S. fuscicollis.*

3) It is predicted that *S. fuscicollis* will be found at a lower mean height than its congener (e.g. Yoneda, 1984a).

4) As *S. fuscicollis* have been reported to be more 'curious' than their congeners, and more liable to approach novel situations (e.g. Box & Morris, 1979; Buchanan-Smith,1989), they would be predicted to make the initial exploration.

5) Animals should be more active (i.e. less resting) in post release, and show a different range of postures as they have a greater potential for movement (i.e. not constrained by small cage size).

6) Substrate use should change during post release, as new types and sizes of substrates are present.

4.9 Methods.

4.9.1 Subjects.

The subjects used were the second mixed-species group (mixed group 3: see Chapter 3 for details) who were mixed together on 21st of June 1993. On June 27th, once it was established that this group had been successfully mixed, they were moved to their new enclosure.

4.9.2 Housing.

The area where the group was scheduled to free-range was part of the 'old zoo' at Belfast, an off-exhibit area used to store, breed and quarantine animals. The group was initially enclosed in a small, purpose built cage (4.6 x 3.1 x 2.5 m), which had two centrally placed heated and insulated boxes (Figure 4.C). The boxes were raised approximately 1m from the ground, and were positioned in the middle of the raised platform.

The enclosure was built around a tree, and there were various branches attached between the platform and tree, in order to allow the species to become familiar with the route from nest box to tree. The tree itself was connected by means of its branches to the wooded area where the group was expected to range, and it was hoped that acclimatisation to this route would successfully facilitate the groups' safe return from ranging.

The enclosure was constructed on a slope, and had a wooden frame around which 1cm square plastic netting was attached. This arrangement had been successfully used for tamarin groups in the past (see Chapter 3), and was once again adequate for this study. The group was allowed to remain in their enclosure for a period of four weeks, to acclimatise them.

4.9.3 Baseline Procedure.

Between 27th of July and 6th August 1993, the mixed group was observed for a total of 32 hours. All of the observations were carried out by a second observer (R.Day) who was extensively practised in the procedures and who had a high degree of inter-observer reliability with me. He had also extensively practised the estimation of distances and was reliable in this measure (see Chapter 3).

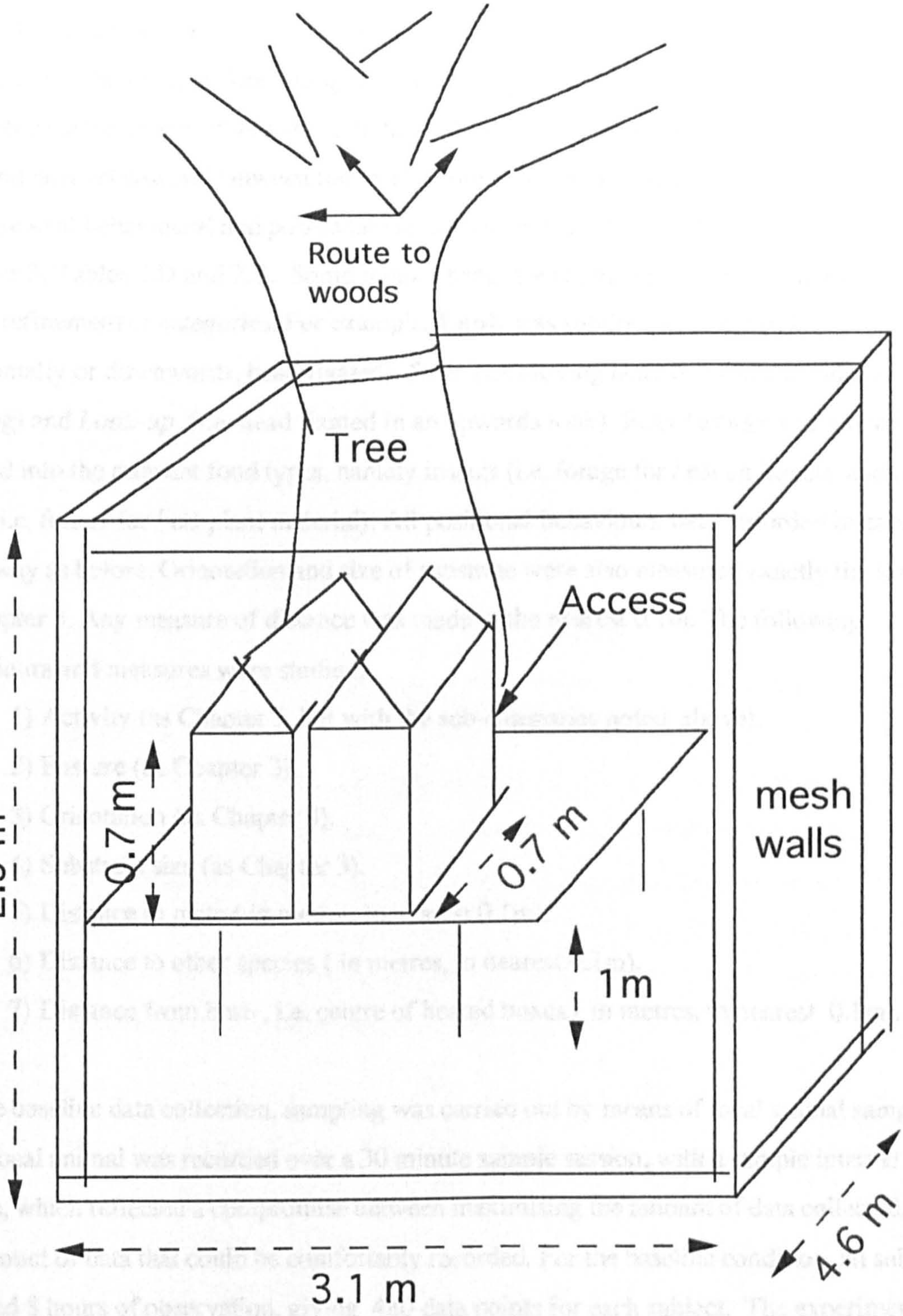


Figure 4.C : Plan of new enclosure for free-ranging mixed-species tamarin group.

Focal animal sampling.

It was first necessary to gain information on the baseline activity budgets and level of interaction in the group before letting them free-range, in order to determine how the experience affects them. It was also felt that continuity of data was important, both between the pre- and post-release and between the work in other chapters of this study. Therefore, the same general behavioural and positional categories were used throughout, as outlined in Chapter 3, Tables 2.D and 2.E. Some minor changes were made, but they were only regarded as the refinement of categories. For example, **Look** was subdivided into *Look* (i.e. stare horizontally or downwards, head fixated), *Scan* (i.e moving head from side to side, while looking) and *Look-up* (i.e. head fixated in an upwards look). Both **forage** and **eat** were divided into the relevant food types, namely insects (i.e. forage for / eat an insect) and plant parts (i.e. forage for / eat plant material). All positional behaviours were recorded in exactly the same way as before. Orientation and size of substrate were also measured exactly the same as in Chapter 3. Any measure of distance was made to the nearest 0.1m. The following behaviours and measures were studied,

1) Activity (as Chapter 3, but with the sub-categories noted above).
2) Posture (as Chapter 3).
3) Orientation (as Chapter 3).
4) Substrate size (as Chapter 3).
5) Distance to mate (in metres, to nearest 0.1m).
6) Distance to other species (in metres, to nearest 0.1m).
7) Distance from base , i.e. centre of heated boxes (in metres, to nearest 0.1m).

For the baseline data collection, sampling was carried out by means of focal animal sampling. Each focal animal was recorded over a 30 minute sample session, with a sample interval of 1 minute, which reflected a compromise between maximising the amount of data collected, and the amount of data that could be comfortably recorded. For the baseline condition, all subjects received 8 hours of observation, giving 480 data points for each subject. The experiment design was counterbalanced, with the order of observation of subjects being randomly varied. Subjects were observed daily between 1000 and 1600 hours, with half of the observations in the morning (1000-1300h) and half in the afternoon (1300-1600h). Behaviours were marked onto a purpose designed checksheet that was suitable for both pre- and post-release. The animals were fed at 0930h, before any observations took place and this was maintained through the course of the study.

Interactions

In addition to the behavioural categories above, any interaction between the members of the different species was noted ad libitum when they occurred, as follows ;

1) What individuals were involved (ID's)
2) What was the nature of the interaction (aggressive or friendly
3) What exactly was the event ?
    i) displacement
    ii) fight
    iii) groom
    iv) huddle, etc.
4) Area where interaction took place (i.e. near to one species food/ nest box etc).

These interactions were noted when they were observed, and were taken regardless of whether or not the individuals' involved were the current focal individual.

4.10 Preparation for release.

Prior to the release, it was necessary to construct a map of the immediate area, and to measure the height of some of the vegetation in the wooded area. This was carried out by means of a measuring tape, and a scale drawing of the site was produced (Figure 4.D). The map contained a series of landmarks and marked trees, so that positions on the map could be related to actual positions. Also, a series of guide marks were painted onto the pathways, to help with estimation of distances. Tree and plant species present in the study area were identified and their positions were noted. Finally, a grid was constructed and placed on the map, and the area was divided into 2 x 2 m quadrats. This meant that relative positions of plants and the mixed group could be established on the map.

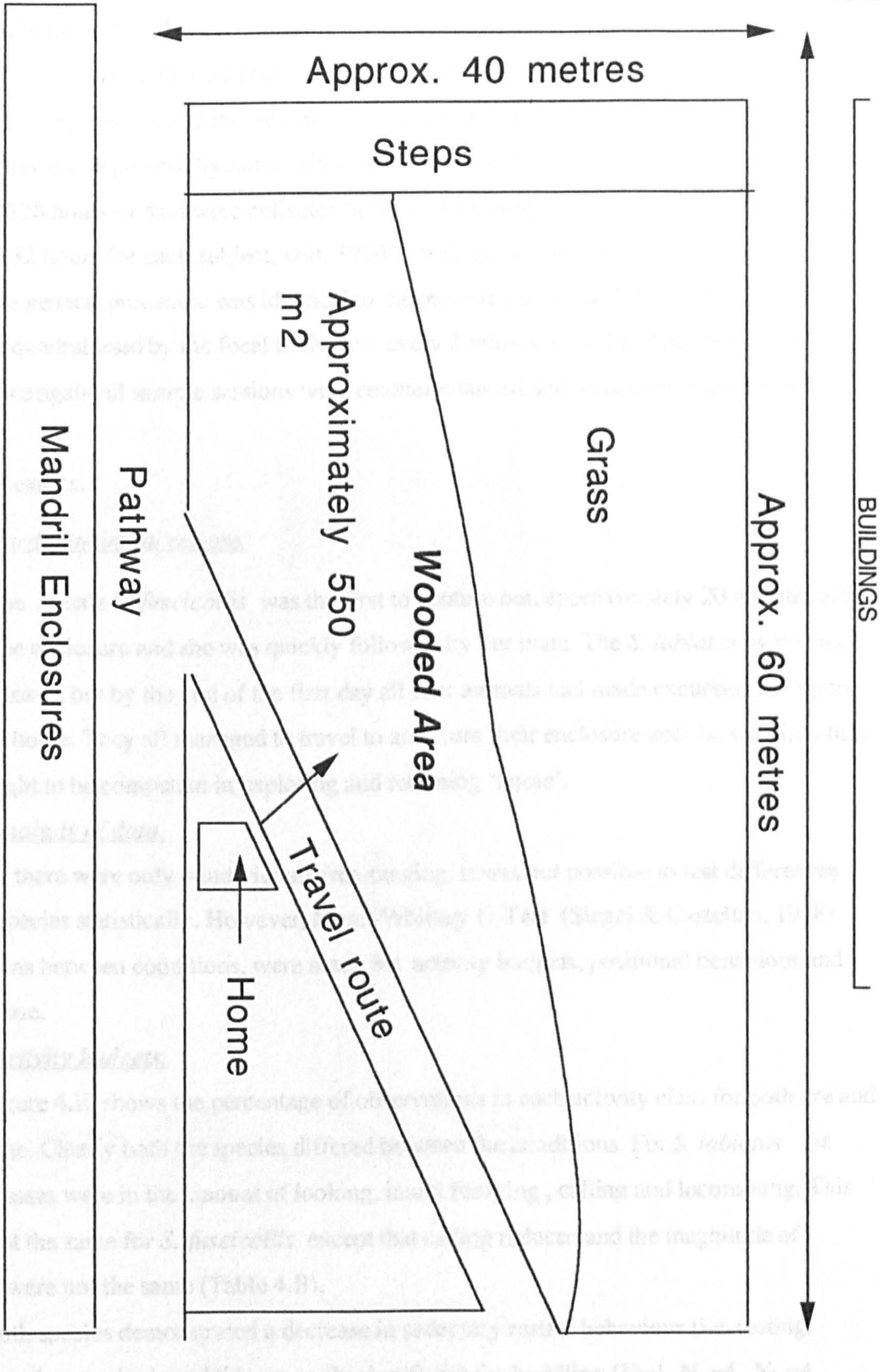


Figure 4.D : Schematic map of wooded area used by free-ranging tamarins at Belfast zoological gardens, not shown to scale.

4.11 Release procedure.

After 28 days in the new enclosure, on the 11th of August 1993, the top of the enclosure was opened beside the tree, and the animals were allowed to leave when they desired. They could potentially range within the zoo grounds for distances up to 1 kilometre. A total of 128 hours of data were collected between 11th August and 17th of October 1993. This gave 32 hours for each subject, with 1920 sample points on each.

The general procedure was identical to the pre-release, but with the added measure of noting the quadrat used by the focal individual every 2 mins, giving 1920 position sample points. Once again all sample sessions were counterbalanced and were controlled for order effects.

4.12 Results.

4.12.1 Reaction to initial release.

The female *S. fuscicollis* was the first to venture out, approximately 20 minutes after opening the enclosure and she was quickly followed by her mate. The *S. labiatus* were much slower to leave, but by the end of the first day all four animals had made excursions of up to 30m from home. They all managed to travel to and from their enclosure and the wood, so they were thought to be competent in exploring and returning 'home'.

4.12.2 Analysis of data.

As there were only 4 individuals free-ranging, it was not possible to test differences between species statistically. However, Mann-Whitney U-Test (Siegel & Castellan, 1988) comparisons between conditions, were made for activity budgets, positional behaviour and substrate use.

4.12.3 Activity budgets.

Figure 4.E shows the percentage of observations in each activity class for both pre and post-release. Clearly both the species differed between the conditions. For *S. labiatus* the main increases were in the amount of looking, insect foraging, calling and locomoting. This was almost the same for *S. fuscicollis* except that calling reduced and the magnitude of increases were not the same (Table 4.B).

Both species demonstrated a decrease in sedentary restful behaviour (i.e. resting, huddling and grooming), and this was only significant for huddling ($U=1$, $N_a=4$, $N_b=4$, $p<0.05$).

Figure 4.E (I) : Activity pattern in S.labiatus pre and post-release

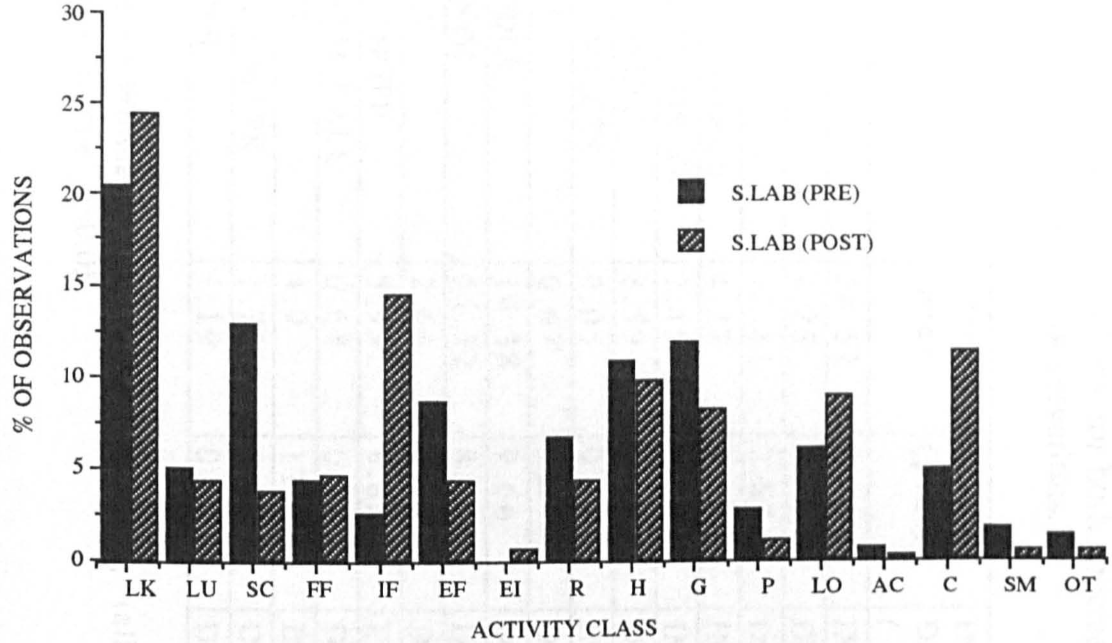
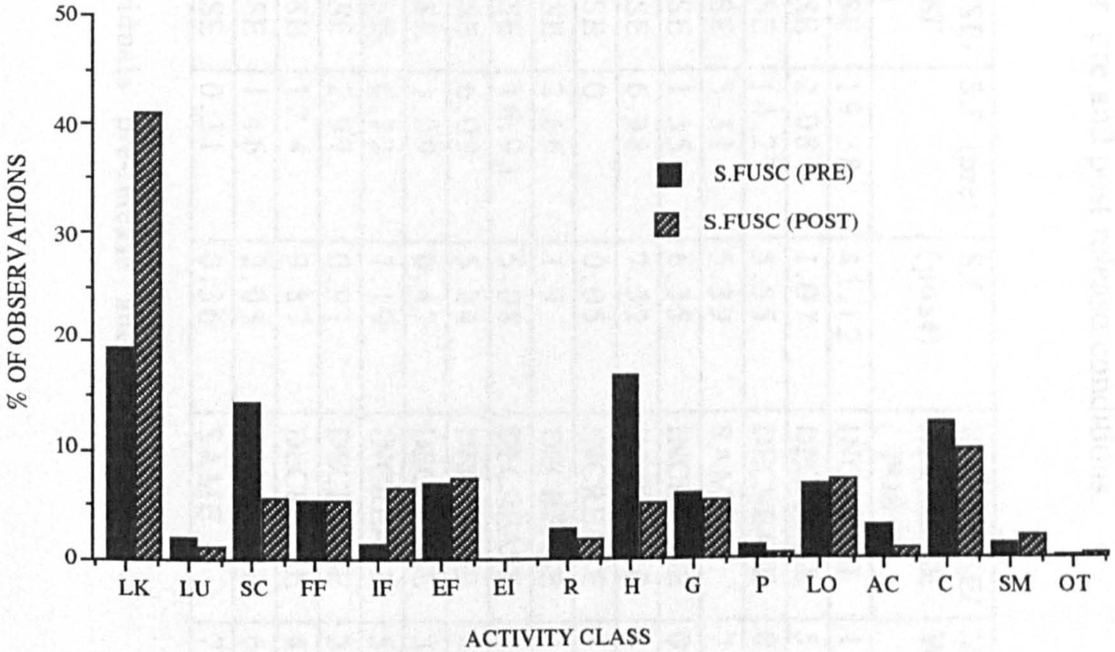


Figure 4.E (II) : Activity pattern in S.fuscicollis pre and post-release



KEY

LK = Look , LU = Look-Up, SC = Scan, FF = Forage for Fruit, FI = Insect forage, EF = Eat Fruit, EI = Eat Insects, R = Rest, H = Huddle, G = Groom, P = Play, LO = Locomote, AC = Alarm Call, C = Call, SM = Scent Mark, OT = Other behaviour

Table 4.B : Activity budgets for both species, under pre and post release conditions. Values are percentage of observations.

	S.lab (pre)	S.lab (post)	INCREASE/ DECREASE (POST)	S.f (pre)	S.f (post)	INCREASE/ DECREASE (POST)	Mann-Whitney U-Test*	Sig**
LOOK	20.52	24.48	INCREASE	19.38	41.12	INCREASE	1	SIG
LOOK UP	4.95	4.22	DECREASE	2.08	1.07	DECREASE	5	NS
SCAN	12.81	3.67	DECREASE	14.27	5.55	DECREASE	0	SIG
FRUIT FORAGE	4.27	4.53	INCREASE	5.31	5.39	SAME	7	NS
INSECT FORAGE	2.45	14.38	INCREASE	1.35	6.35	INCREASE	0	SIG
EAT FRUIT	8.59	4.24	DECREASE	6.98	7.32	INCREASE	4	NS
EAT INSECTS	0.05	0.49	INCREASE	0	0.05	INCREASE	1	SIG
REST	6.67	4.24	DECREASE	2.66	1.9	DECREASE	4	NS
HUDDLE	10.38	9.66	DECREASE	16.93	5.08	DECREASE	1	SIG
GROOM	11.72	8.15	DECREASE	6.09	5.34	DECREASE	4	NS
PLAY	2.66	0.99	DECREASE	1.09	0.47	DECREASE	3	NS
LOCOMOTE	5.99	8.83	INCREASE	6.72	7.19	INCREASE	5	NS
ALARM CALL	0.68	0.13	DECREASE	2.97	0.91	DECREASE	2	NS
CALL	4.9	11.2	INCREASE	12.4	9.87	DECREASE	4	NS
SCENT MARK	1.72	0.36	DECREASE	1.46	2.03	INCREASE	6	NS
OTHER	1.19	0.42	DECREASE	0.31	0.36	SAME	7.5	NS

* Mann-Whitney U-test, Na= 4, Nb=4, (all individuals pre-release and post-release).
**Significance p=0.05.

Sedentary behaviour was slightly larger for *S. fuscicollis* who had a reduction in restful behaviour from 25.7% to 22.1%. There was a significant increase in the amount of looking ($U=1$, $N_a=4$, $N_b=4$, $p<0.05$). Also, scanning decreased significantly between conditions ($U=0$, $N_a=4$, $N_b=4$, $p<0.05$), but not looking-up ($U=5$, $N_a=4$, $N_b=4$, non-significant). Overall, *S. fuscicollis* had an increase in total vigilance and *S. labiatus* had a reduction.

Both species spent a similar amount of time foraging for fruit, but *S. labiatus* spent less time actually eating it. The two species both had an increase in the amount of time spent foraging for insects, and this was significantly greater after release ($U=0$, $N_a=4$, $N_b=4$, $p<0.05$). Both species were fairly adept at capture, and the subjects spent significantly more time eating insects post-release ($U=0$, $N_a=4$, $N_b=4$, $p<0.05$), although *S. labiatus* caught and ate more. However, most were small flying insects (Flies ; *Diptera spp.*) which were consumed very quickly and did not often coincide with sample points. The two species differed in the way that they tried to capture insects ; *S. fuscicollis* were not proficient at "seize and capture", and spent much time trying to grasp flies in their hands, while not moving their bodies. *S. labiatus* were much more proficient, and spent time visually following the flight of flies, watching them land, and then thrust their bodies forward while grasping with their legs. They were almost always successful when pouncing on the insects (Day, pers. comm.).

Locomotion increased for both species ($U=5$, $N_a=4$,$N_b=4$, non-significant). All individuals reduced the amount of playing and alarm calling after release, but both these measures were not significant ($U=3$, $U=2$ respectively, $N_a=4$, $N_b=4$, non-significant). Calling decreased and scent marking increased for *S. fuscicollis* after release, while the converse was true for *S. labiatus.* Overall both species differed in their activity budgets after release and there was a general increase in active behaviour. The two species differed in some aspects of activity, but much of it was in magnitude of effect, with 11/16 activities showing the same direction of change.

4.12.4 Positional behaviour.

Positional behaviour was not as divergent between conditions as activity, and differed only slightly between species (Figure 4.F). Most individual behaviours occurred in low frequencies for both species and the main difference was an increase in the amount of sitting post-release. Sitting increased for every individual but overall this was not significant ($U=4$, $N_a=4$, $N_b=4$, non-significant). Other differences between conditions were found (Table 4.C). For example, even though both species increased their amount of locomotion post release, the preferred postures used were different.

Figure 4.F (I) : Positional behaviour in S.labiatus pre and post-release

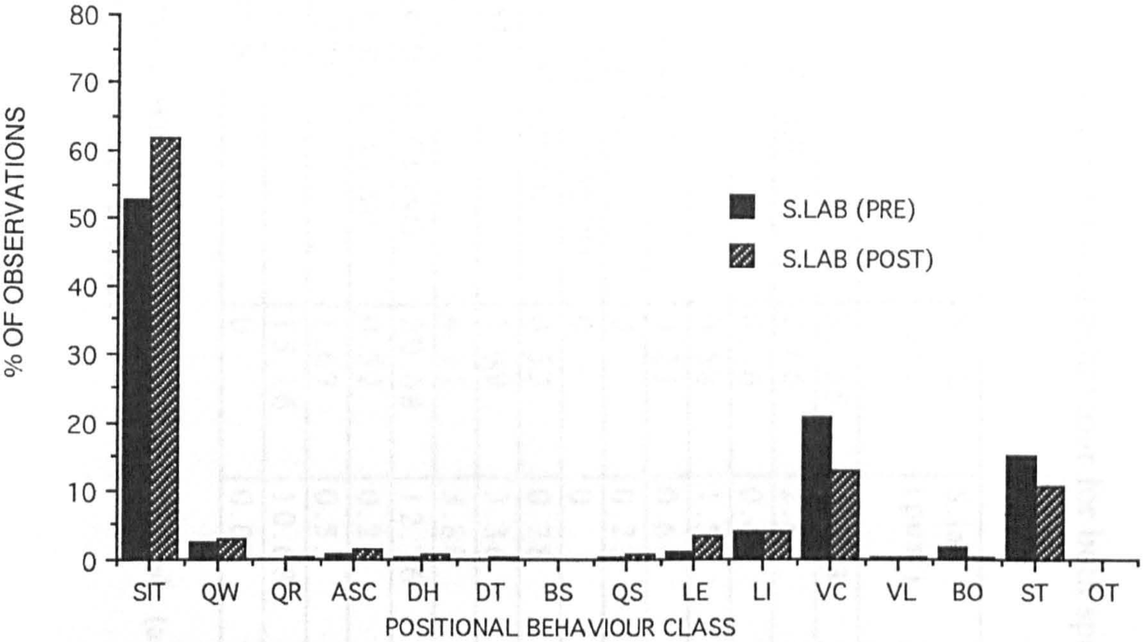
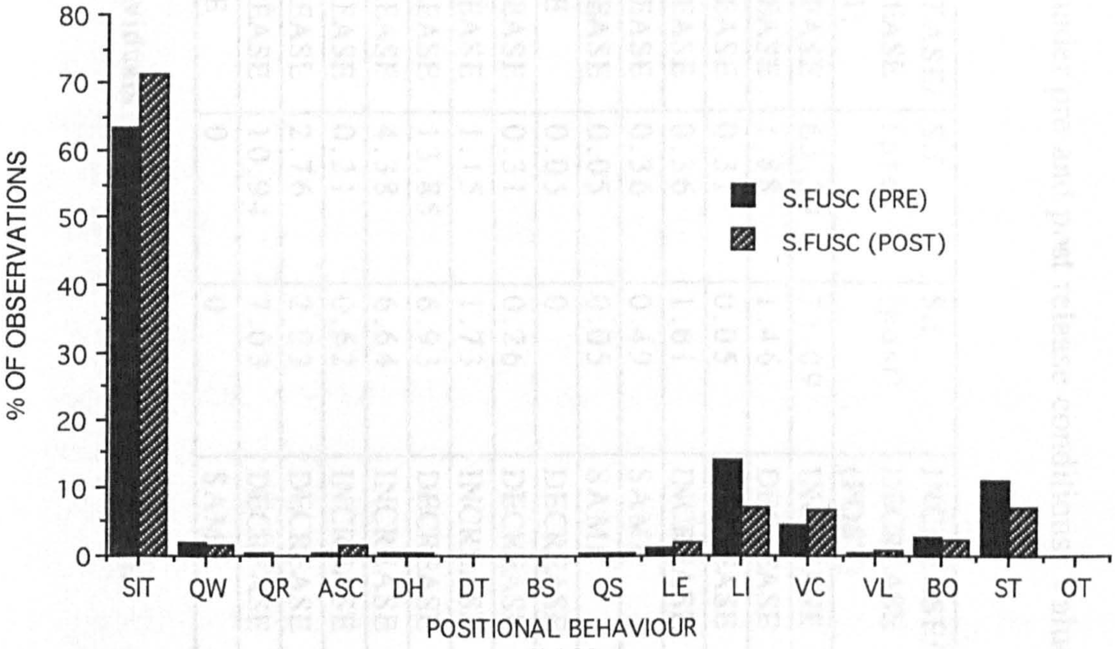


Figure 4.F (II) : Positional behaviour in S.fuscicollis pre and post-release



KEY

SIT = Sit, QW = Quadrupedal Walk, QR = Quadrupedal Run, ASC = Ascend, DH = Descend Head First, DT = Descend Tail First, BS = Bipedal Suspension, QS = Quadrupedal Suspension, LE = Leap, LI = Lie, VC = Vertical Cling, VL = Vertical Leap, BO = Bound, ST = Stand, OT = Other Position.

Table 4.C : Positional behaviour for both species, under pre and post release conditions. Values are percentage of observations.

	S.lab (pre)	S.lab (post)	INCREASE/ DECREASE (POST)	S.f (pre)	S.f (post)	INCREASE/ DECREASE (POST)	Mann-Whitney U*	Sig**
SIT	52.55	63.03	INCREASE	63.39	71.09	INCREASE	4	NS
QUAD WALK	2.66	2.84	INCREASE	1.88	1.46	DECREASE	8	NS
QUAD RUN	0.16	0.47	INCREASE	0.31	0.05	DECREASE	7.5	NS
ASCEND	0.68	1.51	INCREASE	0.36	1.61	INCREASE	0	SIG
DESCEND HF	0.21	0.68	INCREASE	0.36	0.49	SAME	1	SIG
DESCEND TF	0	0.23	INCREASE	0.05	0.05	SAME	2	NS
BIPEDAL SUSPEND	0	0	SAME	0.05	0	DECREASE	6	NS
QUAD SUSPEND	0.52	0.78	INCREASE	0.31	0.26	DECREASE	6	NS
LEAP	1.09	3.36	INCREASE	1.15	1.73	INCREASE	4	NS
LIE	4.11	3.88	DECREASE	13.85	6.93	DECREASE	5	NS
VERTICAL CLING	20.68	12.76	DECREASE	4.38	6.64	INCREASE	8	NS
VERTICAL LEAP	0.52	0.21	DECREASE	0.21	0.62	INCREASE	7	NS
BOUND	1.67	0.55	DECREASE	2.76	2.03	DECREASE	6	NS
STAND	15.16	10.68	DECREASE	10.94	7.03	DECREASE	1	SIG
OTHER	0	0.03	SAME	0	0	SAME	6	NS

* Mann-Whitney U-Test, Na=4, Nb=4 (all individuals pre-release and post-release).
**Significance p=0.05.

S. labiatus had an increased amount of quadrupedal walking, quadrupedal running and leaping, while vertical clinging & leaping and bounding were reduced post-release. *S. fuscicollis* had a reduction in quadrupedal walking, quadrupedal running and bounding, with an increase in vertical clinging & leaping and leaping. So overall differences between the conditions were not significant (see Table 4.B).

All individuals spent significantly more time ascending ($U=0$, $N_a=4$, $N_b=4$, $p<0.05$) and descending substrates head first ($U=1$, $N_a=4$, $N_b=4$, $p<0.05$) during the post-release stage, thus reflecting the use of higher substrates. Other differences occurred after release, where both species showed an increased, but non-significant, amount of descending and lying. All individuals spent significantly less time standing post-release ($U=1$, $N_a=4$, $N_b=4$, $p<0.05$). The *S. fuscicollis* spent more time vertically clinging, while the *S. labiatus* actually had a reduction in this posture. The reduction in standing and lying can be related to the lessened resting time in nest boxes, which was probably replaced by sitting (while looking).

4.12.5 Substrate use.

Substrate use changed after release (Table 4.D). There was a significant increase in the use of obliquely orientated substrates, from 4.3% to 31.8% for *S. labiatus* and from 8.9 to 26.1% for *S. fuscicollis* ($U=0$, $N_a=4$, $N_b=4$, $p<0.05$). Both had a reduced use of horizontal substrates by approximately 20% post-release, and this was significant ($U=1$, $N_a=4$, $N_b=4$, $p<0.05$). Vertical substrates were used less often by *S. labiatus* and slightly more often by *S. fuscicollis* upon release, so differences were non-significant ($U=8$, $N_a=4$, $N_b=4$, non-significant).

These changes can probably be related to the presence of an increased amount of oblique substrates. For both species, all substrate size use changed significantly after release (Table 4.D). Pre-release substrate use of over 90% large substrates was significantly reduced to approximately 50% upon release ($U=0$, $N_a=4$, $N_b=4$, $p<0.05$). Medium sized substrates (not present pre-release) were used for around 7% of observations and small sized substrates were used for the remaining 40-50% of time. Both these changes were significant ($U=0$, $N_a=4$, $N_b=4$, $p<0.05$).

Both the orientation and size of substrates changed substantially after release and the naturally occurring small, obliquely angled substrates were now used by the two species.

Table 4.D : Substrate use in two free ranging species of tamarins, both pre and post-release. Values are percentage of observations in category.

Orientation	S.L. (PRE)	S.L. (POST)	Increase / Decrease	S.F. (PRE)	S.F. (POST)	Increase / Decrease	Mann Whitney* U	Sig**
Horizontal	74.22	54.51	Decrease	86.67	65.78	Decrease	1	SIG
Oblique	4.27	31.77	Increase	8.85	26.09	Increase	0	SIG
Vertical	21.51	13.72	Decrease	4.48	8.12	Increase	8	NS
Size								
Small	3.8	49.56	Increase	6.46	42.66	Increase	0	SIG
Medium	0	6.95	Increase	0	6.3	Increase	0	SIG
Large	96.2	43.49	Decrease	93.54	50.72	Decrease	0	SIG

* Mann-Whitney U-Test, Na=4, Nb=4, (all individuals pre-release and post-release).
**Significance p=0.05.

4.12.6 Height use.

Height use was compared both pre and post-release (Table 4.E). In the pre-release condition the two *S. labiatus* had a slightly higher mean height and consequentially a higher mean species height, but this was only by a very small amount. After release the subjects had a significantly higher mean height ($U=0$, $N_a=4$, $N_b=4$, $p<0.05$), reflecting the increased availability of substrates. However, in the post-release condition, the female *S. fuscicollis* had the highest mean height (2.03 m), while the male *S. labiatus* (1.82m) had a higher mean than the male *S. fuscicollis* (1.72m). The female *S. labiatus* had the lowest mean (1.68m). Therefore, the *S. fuscicollis* had a higher mean height than the *S. labiatus*. The much higher height of the female *S. fuscicollis* was the main difference, but height use varied throughout the study (Figure 4.G).

Table 4.E : Mean height used per subject, means are calculated from all sample points, N = 960 sample points pre-release, and N =1920 sample points post-release, for each subject.

	S. labiatus			*S. fuscicollis*		
	Male	Female	**Both**	Male	Female	**Both**
Pre-Release Mean	1.08 m	1.10 m	**1.09 m**	1.04 m	1.07 m	**1.06 m**
Standard Error	0.1	0.1	0.1	0.1	0.1	0.1
Post-Release Mean	1.82 m	1.68 m	**1.75 m**	1.72 m	2.03 m	**1.87 m**
Standard Error	0.2	0.2	0.2	0.3	0.3	0.3

During the course of observation days, the mean height used by each species varied depending upon what activities were conducted and towards the end of the study, the *S. labiatus* were found at a higher height more often (Figure 4.G).

As the group was part of a developing situation (i.e. adapting to a new situation) and was part of a small sample size, it is perhaps too early to determine if captive *S. fuscicollis* are usually found at a higher or lower level than *S. labiatus.*

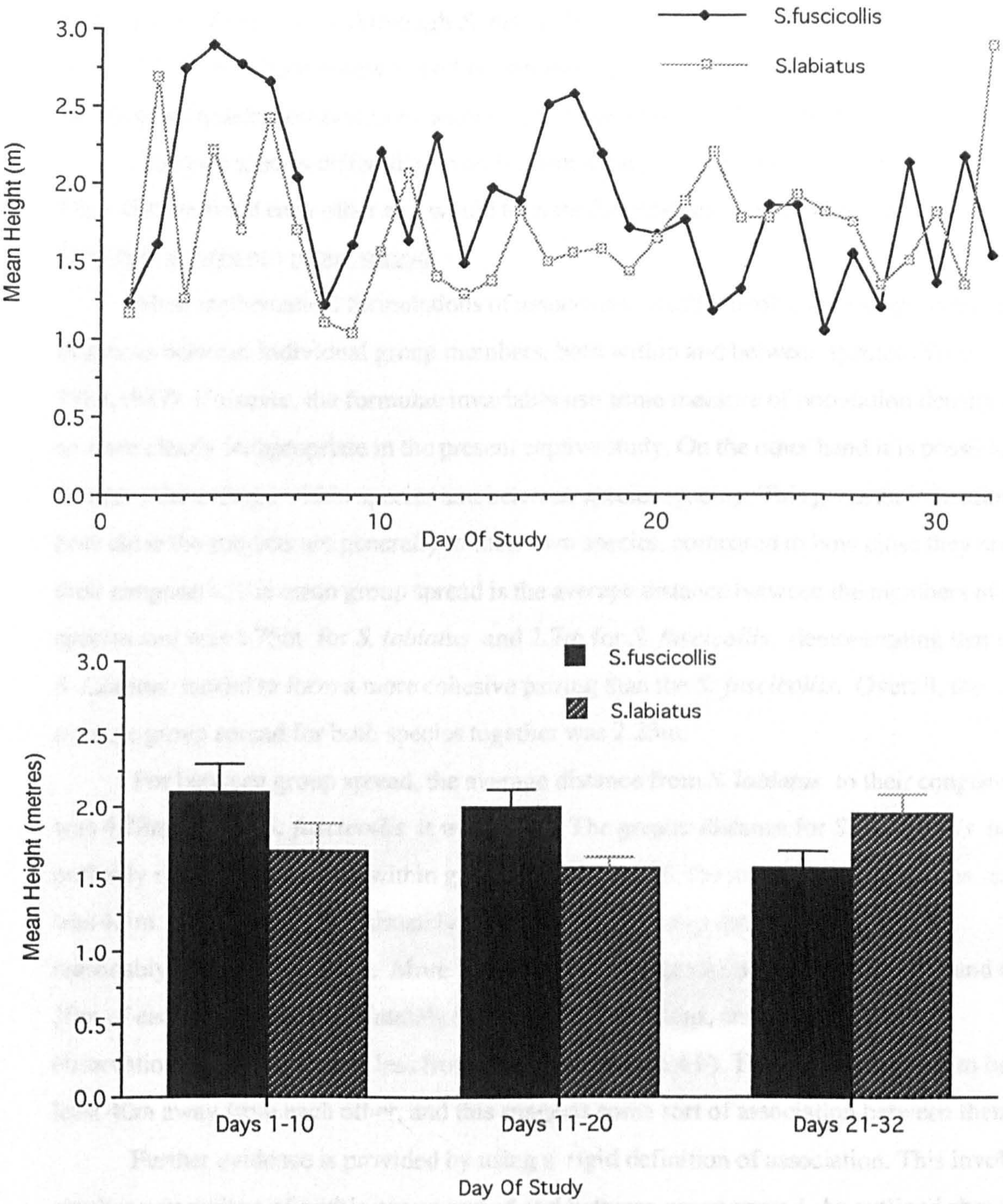


Figure 4.G : Mean daily height use per species, over 32 days post-release. Upper graph shows the Variation over the whole study, while the lower graph shows mean values for 3 time periods, and bars show standard errors.

4.13 Measures of association.

1) Range use. Both species used 134 different 2 x 2m quadrats, 53% of these were used by both species (Figure 4.H). Although *S. fuscicollis* used 35 more quadrats, both species only spent 13.8 % of sample points in exclusively used quadrats. This means that approximately 86.2% of all quadrat observations were when the species were in quadrats that they both used.

The two species differed in overall quadrat use, but spent most time in the shared area. They did not avoid each other and would tolerate the other species in the shared area.

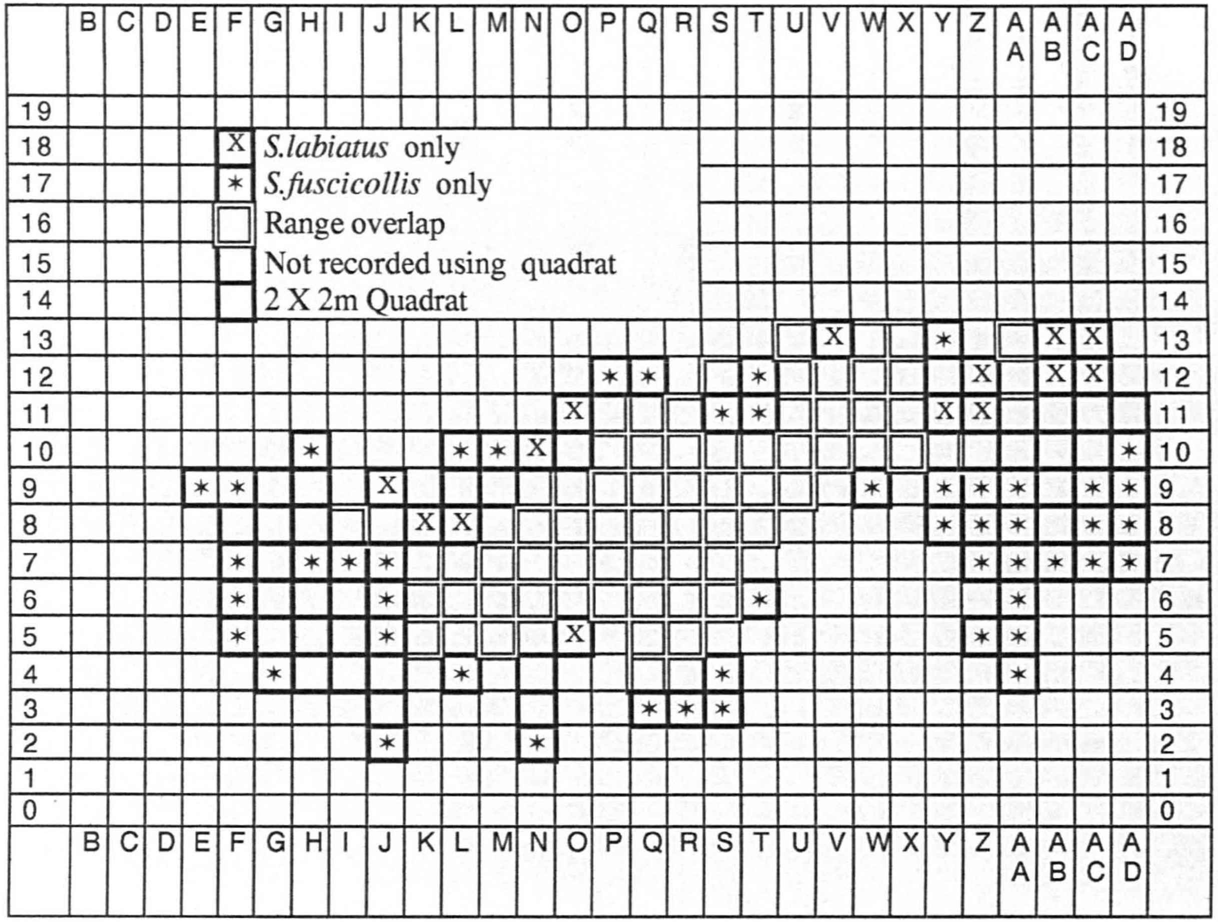
2) Within & between group spread.

Most mathematical formulations of association usually involve the interpretation of distances between individual group members, both within and between species (Waser, 1982, 1984,1987). However, the formulae invariably use some measure of population density and so were clearly inappropriate in the present captive study. On the other hand it is possible to compare the average within species and between species spacing. This gives an indication of how close the subjects are generally to their own species, compared to how close they are to their congeners. The mean group spread is the average distance between the members of each species and was 1.75m for *S. labiatus* and 2.7m for *S. fuscicollis*, demonstrating that the *S. labiatus* tended to form a more cohesive pairing than the *S. fuscicollis.* Overall, the average group spread for both species together was 2.23m.

For between group spread, the average distance from *S. labiatus* to their congeners was 4.28m and for *S. fuscicollis* it was 4.78m. The greater distance for *S. fuscicollis* is probably related to the larger within group spread. Overall, the mean distance between species was 4.5m. This is only approximately twice the within group spread and indicates a reasonably close coordination. More impressive is the fact that both species were found within 10m of each other for approximately 90% of all observations, and in some 65% of observations they were 5m or less from each other (Table 4.F). They had a potential to be at least 40m away from each other, and this suggests some sort of association between them.

Further evidence is provided by using a rigid definition of association. This involves another comparison of within group spread and between group spread. As outlined above, the use of the formulae developed for testing association in wild animals are problematic. However, other studies of sympatric primate species use a definition of association that was similar to (e.g. Oates & Whitesides,1990; Whitesides,1989) or slightly greater than (e.g. Buchanan-Smith,1989; Struhsaker,1981) mean group spread.

Figure 4.H : Range overlap and quadrat use in 2 species of free-ranging tamarins. Values are based on position of focal individual at 2 minute sample intervals.



By using the mean within group spread as a criterion for association, this gives a more stringent measure of association than some previous studies (Peres,1991; Pook & Pook, 1982), while still giving a reasonable indication of the time spent in association. Consequently, the mean within group spread of the two species (2.23m) was now the criterion with which I defined association.

TABLE 4.F : Within species spread and between species spread, in two species of free-ranging tamarins. Distances are summed for species, and are for post-release data only.

	0 cm	≤ 0.2 m	≤ 0.5 m	≤ 1.0 m	≤2.25 m	≤ 5 m	≤ 10 m
Within Species Spread (%)	26.1	31.3	39.2	60	71.2	85.1	97.9
Count	2006	2401	3012	4610	5467	6536	7518
Between Species Spread (%)	1.0	2.1	5.4	40.4	49.3	64.7	89.4
Count	80	160	414	3103	3784	4968	6867

Nearly half of all between species distances were found to lie under this new criterion (Table 4.F). Indeed in 40% of all observations the species were found at distances of 1 metre or less apart. The two species had few close interactions, and were found within 50cm of each other in only 5% of observations. However, they were found within this distance of their own species on 40% of observations.

The above data show that the two species shared much of the wooded area, both in time and space and were found close to each other for much of the time. A strict definition of association, relating within species spread to between species spread, demonstrated an association of 49.3% of time. The two species did form an association, but retained their own separateness by having most intimate contact with their own species.

4.14 Relative "Curiosity".

The *S. fuscicollis* can be said to be more curious for three reasons :

1) The female made the initial foray into the wooded area, followed by her mate. It was only subsequently the *S. labiatus* ventured out.

2) They used a greater number of different quadrats than the *S. labiatus*, and they were found to venture to the extremes of the area (Figure 4.H). *S. labiatus* concentrated on the central areas more.

3) On two occasions the female ventured outwith the main wooded area (Figure 4.D), and travelled a distance of more than 150 metres from the home cage to the "old marmoset house" (from where she was caught up and returned). The other animals were never seen to range this far.

4.15 Interactions.

Table 4.G shows the interactions between the species. Displacements and aggression were the most common forms of interaction, followed by huddling and calling. Concentrating on the direct interactions (excluding calling) these can be divided into agonistic (i.e. aggression & displacement) and friendly (i.e. huddle, play, groom, solicitation & copulation). It is clear that *S. labiatus* were responsible for most agonistic encounters, initiating 87.6% of all such actions, which consisted of 54% of all interactions. They were also responsible for 70.4% of all friendly acts, comprising around 20% of total interactions.

Table 4.G : Interspecific interactions between members of a free-ranging mixed-species tamarin troop, at Belfast zoological gardens.

	S. labiatus	*S. fuscicollis*	Total	Percentage
Displacement	52	1	53	29.44%
Aggression	33	11	44	24.44%
Huddle	25	7	32	17.78%
Call	3	26	29	16.11%
Play	8	5	13	7.22%
Groom	3	2	5	2.78%
Solicitation	1	0	1	0.56%
Copulation	0	1	1	0.56%
Tongue flick	0	1	1	0.56%
Other	1	0	1	0.56%

S. fuscicollis directed most calls towards *S. labiatus.* Often these calls were around agonistic events. Overall *S. labiatus* initiated most interactions and displaced *S. fuscicollis* from desired areas and objects. These were usually preferred feeding sites, such as laurel leaves, found first by the *S. fuscicollis,* but subsequently taken over by the more dominant *S. labiatus* .

One interesting interaction was a case of interspecific mating. The female *S. labiatus* solicited the male *S. fuscicollis* to mate with her. He duly performed a single act of copulation, which was never seen to be repeated. This may be related to the age of his own mate, who was past breeding and resisted any sexual solicitation and attempted copulations by her partner (Day, pers. comm.). The female *S. labiatus* later gave birth to two still-born infants which were clearly *S. labiatus* and the timing of birth suggested that the interspecific mating occurred when she was already pregnant.

4.16 Discussion.

Previous observations have shown that mixed-species troops of *S. labiatus* and *S. fuscicollis* can be formed in captivity (Hardie *et al.*, 1993; Chapter 3), however, it was not clear whether these "associations" differed from mere mutual toleration in an enclosed area. The data in the present chapter suggest that there is some degree of association between the species and as they could potentially avoid each other, it is suggestive of some degree of sharing space. More pertinent data relate the within to between group spreads. Both species were found as close to each other as the average distance within same species pairs, for around half of all observations. Thus the present study found an association of at least 50% using this very stringent definition of association, and this compares favourably to studies in the wild. For example, other studies of *S. labiatus* and *S. fuscicollis* mixed troops, whatever the definition of association, found groups spent between 50 and 84% of observation time together (see Chapter 2). There were few close contacts between the species, and they were found very infrequently within 50cm of each other, but were found this close to their own species much more often. Few studies measured distances between species, but Norconk (1990b) found that mixed groups of *S. mystax* and *S. fuscicollis* spent little time within 1m (her closest distance measure) of each other. They also spent around one quarter of observations within 1m of their own species. This was a similar pattern to the present study, although absolute distances were different, and reflects the way that the mixed-species group consists of two different species, which remain spatially distinct.

As both free-ranging species shared the wooded area, and had a coincidence in both space and time that exceeded half of observation time, it is arguable that they had formed some sort of association that compared convincingly to those found in wild tamarins. I therefore contend that this group of captive tamarins has formed an association, and this gives a degree of validity to the overall mixed-species project.

In common with the few published accounts of free-ranging tamarins, the present study demonstrated that members of the mixed-species troop were more active post-release (Bronikowski *et al.*, 1989; Price *et al.*, 1989,1991). This increased activity was made up by a reduction in sedentary behaviour, especially resting, and a slight increase in locomotion. This increase in activity has also been found when captive-born and reared primates have been allowed access to outdoor areas (e.g. Bowen,1980; Clarke *et al.*, 1982; Chamove & Rohrhuber, 1989; O'Neill *et al.*, 1991). Similarly, both species of tamarins also showed a change in the range and pattern of positional behaviour. These overall changes were predicted and suggest that the animals may have benefited from the experience of release by their corresponding flexibility in behavioural repertoire (Box,1991c). As the species had changed behaviour after being released, becoming more active, it can be argued this was a procedure which increased their welfare. Specifically, now the animals were present in a "natural" environment and it is argued that as a result they would likely be using more natural behavioural patterns (e.g. Chamove & Rohrhuber, 1989; Mallinson,1982; Redshaw & Mallinson,1991).

The post-release reduction in amount of total vigilance for *S. labiatus* was strikingly different to the increased vigilance for *S. fuscicollis*. The amount of scanning and looking-up actually reduced for both species, and may represent the species being more secure in a heavily foliated area. This pattern of utilising available foliage has been shown for captive tamarins, which were demonstrated to have a preference for using foliated areas (Ham, unpub. data), while crypticity, where the tamarins colouration makes then blend into their background, has also been suggested as being important in wild tamarins (e.g. Dawson, 1979 ; Neyman,1980). Overall, both species still spent over one third of their time in vigilance, suggesting that this is a very important behaviour to tamarins. In comparison to other studies, the behaviour of the *S. fuscicollis* somewhat resembled that of the free-ranging *S.oedipus* at Jersey Wildlife Preservation Trust, where looking up increased post-release (Price *et al.*, 1991). This type of vigilance was the only behavioural category that was examined both pre and post-release. More detailed data were collected post-release, where they spent around 15% of time looking downwards and approximately 10% of time looking at specific objects. In general, it is clear that as in the present study, vigilance was an important part of the lives of free-ranging *S.oedipus*.

Insect foraging significantly increased post-release for both species and as insects are an important component of wild tamarin diets (e.g. Garber,1993a,b; Peres, 1991; Snowdon & Soini,1988; Yoneda,1981), this can be seen to be beneficial for free-ranging captive-bred animals. The actual capture rate was not measured, but for *S. labiatus* small flying insects were often captured from leaves and branches and *S. fuscicollis* often foraged in trunk holes or embedded insects (Day, pers. comm.). This appears to be similar to the seize and capture methods of wild *S. labiatus* (e.g. Buchanan-Smith,1990a; Yoneda, 1981; Chapter 2) and the extractive foraging of *S. fuscicollis* (e.g. Garber,1993b; Peres,1991; Soini,1987; Chapter 2).

While positional behaviour also changed after release, it was centred around a few particular categories. For example, sitting was the largest single increase, and because the overall amount of active behaviour increased the reason for this was not clear. However, sitting is often the most widely used posture in captive tamarins (Hardie, in prep.; Vogt,1978) and is frequently used during foraging and feeding in wild tamarins (e.g. Garber,1984b). It is also used frequently while animals are being vigilant (cf. Sit & Look: Vogt,1978). Therefore an increase in sitting may be due to the increased range of activity shown by free-ranging tamarins.

Locomotory posture differences between the conditions were related to an increase in general activity and the fact that the animals had a larger area to move within. The between species differences in preferred locomotory postures are similar to those found in the wild. Specifically, *S. labiatus* shows a reliance on quadrupedal progression (i.e. Quadrupedal walking, Quadrupedal running & bounding), while *S. fuscicollis* prefers to use vertical clinging and leaping (e.g. Buchanan-Smith,1990a; Pook & Pook,1982; Yoneda, 1981; Chapter 2). Garber (1994) has recently argued that all tamarins frequently use quadrupedal progression and in the current study both species often used these postures both pre and post-release.

The two species decreased the amount of lying and standing after release, and this can be related to their increased activity. The greater amount of ascending and descending is probably related to an increased use of differently sized and angled substrates.

As predicted, the substrate use changed post-release and immediately it is obvious that both species now used oblique substrates much more, while still using horizontal branches most frequently. The increased use of vertical substrates by *S. fuscicollis* probably reflects the increased use of vertical clinging & leaping. A large use of horizontal and obliquely orientated substrates has been shown in previous studies of captive (Hardie,in prep.) and wild tamarins (Garber 1980a,b,1984b). Size use changed post-release, and there was a tendency to concentrate use on small and large sized substrates. This had been previously found to be the case in at least four wild *Saguinus* species, including *S. labiatus* & *S. fuscicollis* (Garber, 1991; Chapter 2). Overall changes between conditions are mainly reflected by the use of the large number of naturally occurring small oblique branches found in the wooded area.

No clear height differences were found pre-release, but both *S. labiatus* were found at a marginally higher level. Upon release both species all had a significantly higher mean level of height use, but individual variation was high. The result was a higher mean height for *S. fuscicollis* and this was not as predicted. In the wild the *S. labiatus* are found at a higher mean level of the forest (see Chapter 2; Buchanan-Smith,1990a; Pook & Pook,1982), but in the present study the species varied daily on mean height use, using different areas for foraging and feeding. Only larger numbers of subjects and an increased study time will determine if individual variation or species differences occurred.

In common with studies in the wild, the *S. fuscicollis* was almost exclusively dominated by its congener (Heymann,1990b; Norconk,1990b; Peres, 1991; Pook & Pook, 1982). In this study this was evident in displacements and aggression which accounted for over half of all recorded interactions, and these were frequently associated with conflict over food. Most aggressive incidents described in wild tamarins have been over restricted food sources (Heymann, 1990b; Terborgh,1983; Yoneda,1981; Chapter 2), but few friendly interactions are described. Also, no cases of interspecific huddling or grooming have been noted in wild populations (see Heymann,1990b). The only published account of interspecific social grooming in a captive, wild-caught, mixed-species group of *S. mystax* and *S. fuscicollis* , had a rate of less than 1 event per hour (Heymann & Sicchar Valdez,1988). In the present study grooming was even rarer, consisting of only 5 events in 128 hours of observation, so the importance of this in *S. labiatus* and *S. fuscicollis* mixed groups is unclear.

Interestingly, one case of interspecific sexual solicitation and mating was noted between the female *S. labiatus* and the male *S. fuscicollis* . In the wild there are no accounts of such interactions, but again it was found in Heymann & Sicchar Valdez's (1988) study. They describe a sub-adult *S. mystax* attempting to mate with a young *S. fuscicollis* , but regard this as "rare". These attempts at copulation may, or may not , produce viable offspring, but I encountered no reports of hybridisation between *S. fuscicollis* and members of the *S. mystax* group in the literature (e.g. Hershkovitz,1977), suggesting that hybrids are behaviourally and/or physically prevented.

4.17 Overall conclusions.

The behaviour of the free-ranging group (section 4.B) suggests that the behaviour of the 5 mixed-species groups formed in the cage system (section 4.A) were not merely a tolerance of the presence of congeners in an enclosed area, but are essentially mixed-species groups forming associations which have similar key behaviours in common with those found in the wild. For, example, the ecological validity of the present study is enhanced by the finding that in enclosed groups of *S. labiatus*, all individuals used a higher mean height in their enclosure than the *S. fuscicollis* did, thus demonstrating a similar vertical partitioning to their wild counterparts. Also, that the direction of dominance was also equivalent to that shown in wild tamarins, where the members of the *S. mystax* group are always dominant to the *S. fuscicollis.*

Therefore, it appears that the general behaviour of the captive mixed-species tamarins was sufficiently comparable with that found in mixed-species tamarins in the wild, and as a consequence the results of the subsequent experiments conducted in this thesis, are potentially relevant to the overall discussion of the costs and benefits of forming tamarin mixed-species groups.

Chapter 5 : Response of Single and Mixed-Species *Saguinus* Groups to the Introduction of Novel Non Threatening[1] Objects.

5.0 Introduction.

Flexibility of behaviour can be thought of as a way of adjusting to and dealing with environmental change (e.g. Box,1984; Clark,1991; Fragaszy,1979; Fragaszy & Mason,1978). The ability to deal with an unexpected or unknown situation may bring about benefits such as the exploitation of new food sources, but may also involve the participant in some degree of cost. Any response shown to novelty is thought to consist of a complex mixture of factors which vary according to the species involved, and these factors may include attributes of any novel object (colour, shape, size, patterning, etc.), the animals' life-style, experience, cognitive abilities and social grouping (e.g. Bernstein, 1984; Box, 1991a,b,c; Clark,1991; Clarke & Lindburg,1993; Demaria & Thierry, 1988). Nevertheless, it is not surprising that when tested empirically, most captive animals show a willingness to investigate any new area or object within their territory (Box, 1988 ; Glickman & Sroges,1966; Joubert & Vauclair,1986; Menzel, 1969; Menzel & Menzel,1980; Paquette & Prescott, 1988; Visalberghi, 1988), as it makes adaptive sense for the investigation of new objects, in order to discover any beneficial properties and / or dangers that the object may have.

The variation between groups of animals was described in a large study of responses to novel objects in zoo animals, by Glickman & Sroges (1966), who demonstrated that there was an increase in reactivity found when moving up from reptiles to primitive mammals, to rodents then to carnivores and primates. The greatest number of responses were shown by both primates and carnivores, but primates were shown to have a differential pattern of responses when compared to the other groups of animals, including carnivores. Indeed, primates tended to show more visual orientation towards objects and more manual manipulation of objects than carnivores, despite the similarities in overall number of responses. In addition, Glickman & Sroges (1966) found that there were many differences between primates, at the species level.

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[1] Although in principle any novel object might be perceived as a threat, the objects used in this chapter did not induce alarm calls or piloerection, in contrast to the threatening objects discussed in Chapter 6.

They speculated that the way animals behaved was closely related to "environmental factors" (e.g. active foraging and predator avoidance) in their natural habitat (p152). This effectively means that the differences between species were related to differences in their lives under natural conditions (Box,1984, 1988,1991c; Jolly, 1964).

The underlying concept in the above examples, is that primates are more likely to manipulate and visually contact objects placed in their environment, than other animals. This investigation of objects probably helps them to develop plasticity in their behaviour and to discover new properties of objects that can be useful for future survival (Clark,1991). The ability to learn from even a single investigation of an object has been shown in captivity (Menzel & Juno,1982), and it can be hypothesised that the examination of novel stimuli may lead to the discovery of new sources of food. This is likely to vary along the line of species, due to differences in diets, ecology and feeding adaptations (e.g. Jolly, 1964).

This tendency to investigate novel objects can be beneficial to the individual involved, but it can also be of advantage to other individuals and even to other species through learning from the experience of that individual (Fairbanks & McGuire, 1993; Menzel & Menzel, 1979; Menzel & Juno, 1982, 1984). The polyspecific associations of *Saguinus* species allow the possibility of an exchange of behaviour between the species, and / or the opportunity for the congeners to benefit from the responsiveness of the the other species (see Chapter 1). This exchange of information, or "behavioural facilitation hypothesis", has been proposed as one of the forces driving the species to associate (Chapter 1). Although it is usually proposed that one or both species are involved in the knowledge of the position of scarce local food resources (e.g Gartlan & Struhsaker, 1972; Terborgh, 1983), this facilitation has also been applied to the case of one species learning from the responses of the other species to any novel situation (Buchanan-Smith, 1989). Any difference between the species in responsiveness to a novel situation has important implications for the evaluation of the costs and benefits involved in mixed-species associations.

Buchanan-Smith (1990a) studied the association between *S. fuscicollis* and *S. labiatus* in Bolivia, where she provisioned the tamarins with bananas, in order to attract them to the trapping site. Several groups were trapped at different locations, and in all cases the *S. fuscicollis* were the first to exploit the new food resource and to approach the traps. The *S.*

labiatus, on the other hand, only approached the traps after the *S. fuscicollis* had already learnt to exploit the food source, but they soon displaced the less dominant species and took advantage of the new food source. This pattern was also found by Garcia (pers comm.) who provisioned *S. fuscicollis* and *S. labiatus* at a feeding platform. Although the *S. fuscicollis* ate the bananas first, the other species soon benefited from this behaviour, and started to arrive first at the platform and to exclude the *S. fuscicollis* from the platform. A similar pattern was found by Box & Morris (1979) while trapping *S. fuscicollis* and *S. mystax*. The position can be thought of as the associating species gaining from the behaviour of the *S. fuscicollis* and allowing them to take all the immediate costs of investigation (both energetically and in terms of danger), and still being able to reap any new benefits due to their dominance over the *S. fuscicollis*. In a more natural situation, Peres (1991) has shown that *S. fuscicollis* found more small food sources that generally occur lower in the forest, but were usually displaced quickly by the more dominant *S. mystax*. This shows that one species can learn from the other and can gain new food resources by exploiting the behaviour of that other species. This will be examined later in this chapter (Section 5.10).

5.1 Investigation of objects.

Tamarins will investigate and react to the presence of some unknown object in their environment (e.g. Box & Morris,1979; Buchanan-Smith,1989). The main reason for an approach by tamarins is probably to investigate the properties of an object. These properties can be split into at least 3 basic areas ; Is it dangerous, edible and or useful ? (e.g. to shelter in etc.). The "danger" aspects of objects are examined elsewhere (see Chapter 6), and the "usefulness" of objects will not be addressed. The reaction of tamarins towards the presentation of novel non-threatening, non-food objects will be examined firstly (Section 1) and then novel non-threatening food objects will be examined separately (Section 2). The two species are compared both monospecifically and when in mixed-species groups.

5.2 Section 5.1 : Reaction of tamarins to novel non-threatening, non-food objects.

5.2.1 Introduction.

In terms of responsiveness to novel objects, it can be predicted that *S. fuscicollis* may be more responsive than its associating congener, and that they will tend to respond to novel objects quicker than them. In a previous experiment *S. fuscicollis* were shown to detect any novel objects quickly in their environment (Menzel & Menzel, 1979), but unfortunately there is no available evidence about their congeners. In absence of such data, an appropriate line of investigation may be to suggest that associating congeners could potentially be able to benefit from the "curiosity" of *S. fuscicollis.*

Relative curiosity is a difficult concept to measure as it has loaded emotional (e.g. fear) components (Box,1984: 147). It is however, possible to measure concrete behavioural criteria such as approach to within a certain distance of an object, and the level of investigation of the object (Barnett & Cowan,1976). These types of measure allow a quantification of the way subjects respond to novelty that can be compared between individuals, populations and species.

Differences in approach behaviour can be demonstrated to correspond to differences in species specific life-style traits (e.g. Fairbanks, 1993; Fragaszy,1979; Glickman & Sroges, 1966; Jolly, 1964; Menzel, 1962, 1969). For example, Jolly (1964), in a comparative study of prosimians' reactions to "simple object problems", found that the way in which animals reacted to the problems were similar to the way they approached food. She found that "animals whose food is likely to fly away, must watch, bide their time and pounce with precision" (Jolly, 1964 : 568), and argues that species which forage for insects using a visually orientated manner, may exhibit a similar pattern of behaviour when approaching objects. In another example, *Saimiri sciureus* and *Callicebus moloch* were shown to differ in their approach to novel stimuli. *C. moloch* watched the stimulus, usually for a period of time before approaching ; while the *S. sciureus* approached quickly and investigated from a short distance (Fragaszy, 1979). She outlines differences in their social behaviour, and also contrasts the relative inactivity of *Callicebus* with the high level of movement in *Saimiri*, likening this pattern in captivity to their ranging in the wild. Fragaszy (1979) argues that these differences may account for the differences in approach to novel stimuli. Following these examples, it is conceivable that differences in the life-style patterns of wild tamarins will correspond to some level, with their responsiveness to novel stimuli.

As mentioned before, the *S. labiatus* are usually found higher in the forest than their congeners, and they are more rarely found near to the ground (see Chapters 1&2). They also forage for insects by means of a seize and capture technique, in which vision is an important factor (e.g. Yoneda,1981; Chapter 2). The converse is true for *S. fuscicollis*, and they forage by means of manipulative, extractive foraging, which relies on manual exploration (e.g. Buchanan-Smith, 1990a; Yoneda,1984b; Chapter 2). These differences in life-style can lead to a prediction that *S. fuscicollis* may be relatively more likely to contact an object than their congeners, and that to some degree *S. labiatus* may use visual contact more.

However, the fact that the two species show a divergence in mean height in forest, allows further and more specific predictions based on their life-styles. The above evidence of the responsiveness of *S. fuscicollis* relates only to resources and situations occurring in the lower parts of the forest. As they are found in this area more frequently than their congeners, then this responsiveness may be linked to vertical stratification. Peres' (1991) data suggest that *S. fuscicollis* find and / or respond to resources in lower areas of the forest before their congeners. This would lead to the prediction that this species may react more effectively to lower area objects. On the other hand, the associating species have been shown to be first to reach large food resources, mainly found higher up in the forest (e.g. Buchanan-Smith,1990a; Peres, 1991; Terborgh, 1983). This suggests that the *S. mystax* group may be predisposed to react more efficiently to 'higher-up' objects than *S. fuscicollis.*

As both species have been shown to have life-style traits that diverge in terms of preferred mean vertical height in forest, this presumably also relates to responsiveness within these areas. This allows specific predictions to be made regarding the way they may react to novel objects. The specific predictions to be tested are that ;

1) *S. fuscicollis* will (monospecifically) tend to contact novel objects quicker (approach and / or touch) than a congener will in similar circumstances.

2) *S. labiatus* will approach and / or touch higher-up objects quicker than the *S. fuscicollis*, who should be quicker to approach and / or touch lower area objects.

3) A willingness to contact a novel object by *S. fuscicollis* will allow facilitation of approaching and/ or touching by the congeners (during mixed-species trials) and their latencies will change compared to the monospecific trials.

The subjects were tested under 2 separate conditions:

(1) Monospecifically (baseline, non-associating) (2) In association

5.3 Methods.

Experiment 5.1A The monospecific presentation of novel objects.

Do the 2 species of tamarins react differently to a series of novel objects ?.

5.3.1 Subjects.

The groups tested in this study were 6 groups of *S. labiatus* (SL1, SL2, SL3, SL4, SL5, SL6) and 7 groups of *S. fuscicollis* (SF1, SF2, SF3, SF4, SF5, SF6, SF8), each housed in individual indoor / outdoor cages at Belfast Zoological Gardens. Exact details of groups are presented earlier (see Chapter 3).

5.3.2 Pilot study.

Initially it was hoped to test all groups in the large new cage at the end of the enclosure, so as to standardise position and substrates. Unfortunately, when new groups were first allowed into the area, they were very nervous and failed to adjust quickly to the new surroundings. They would not react to the presence of novel objects in the large area, and so it was inappropriate to test them there. It was necessary to test the animals in their own small "home cages". A pilot study was conducted using groups of both species not being used in the experiment. This indicated that these species would readily react to any novel objects placed in and on the cage frame. This procedure yielded a test protocol that was satisfactory.

5.3.3 Testing protocol.

Object Details : Testing involved recording the reaction of the subjects to the presence of a novel (non-threatening) object presented to them. Each object was chosen from a potential set of around 40 small objects (see Appendix 2), and all animals were presented with the same stimuli in the same area, but not necessarily on the same day. The object presented was assumed to be a novel one and was used for one trial only, and no two objects were placed in exactly the same spot. All objects assigned to an area were positioned in a unique but broadly equivalent area. Only one object was placed into the cage on each separate day. All groups were tested in a standardised procedure, with the same objects being tested in the same area for all groups. Time of day was controlled for by presenting half of the stimuli in the morning and the other half were presented in the afternoon. The general procedure for each session was based on the procedure of Menzel & Menzel (1979) and was as follows :

Object presentation : There was a distinction made between 3 classes of object presentation conditions :

i) On the ground (Floor) ; the object was placed on the floor of the cage, approximately 1m or less from the front of the cage (Plate 6).

ii) On a branch, in the middle of cage (Middle) ; object tied to a branch in the central area of the cage, approximately 120-160 cm off the ground, again approximately 1 m from the cage front (Plate 7).

iii) Tied to cage roof (Top) ; object is placed on top of, or tied to the inside top of the cage, again approximately 1m from cage front (Plate 8).

General Procedure : The animals were initially locked into their own inside areas, as were the animals in the cages adjacent to the subjects. The chosen object was placed in the cage at the appropriate area. The trial began when the door between the inside and outside areas was opened by the observer, and this signalled the start of the sample session whereby the observer started his stopwatch. The observer immediately sat down on a chair, some 2m from the cage front and the following measures were noted ;

Time to exit	- latency from the moment of opening the access door until the first animal ventured out.
Approach	- the latency for the first animal to approach (< 15cm) the object.
Touch	- the latency for the first animal to touch the object, either with arm or by sniffing the object.

If the approach and touch were almost simultaneous (i.e. less than 1 second between them) then they were scored as such, otherwise 2 separate measures were noted. Each trial lasted until all the behaviours were carried out, or until 30 minutes duration from the opening of the door had been reached. If the subjects did not approach and / or touch the object within the 30 minutes, it was scored as a failure. Observations were only conducted on dry, mild days (i.e. temperature > 12^{o}c) and each group were presented with 6 objects in each of the 3 placement areas, split equally over mornings and afternoons. The study was conducted during two separate periods ; May - July 1993, and April-June 1994. All groups received presentations of the same objects, in the same areas at the same time of day, thus reactions to individual objects were directly comparable between groups.

Plate 6 : An example of a floor area object placement.

Plate 7 : Typical placement for a middle area object.

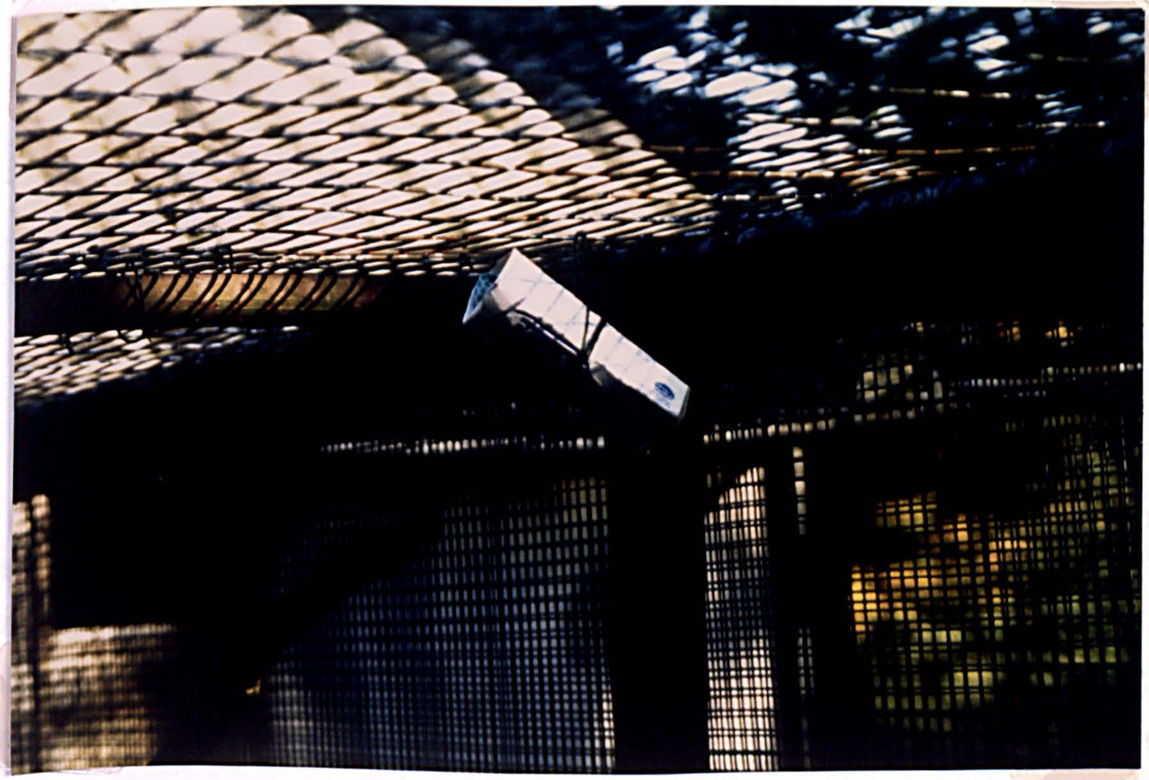


Plate 8 : An example of top area objects.

Data analysis : Individual sample sessions were carried out on separate days and were therefore considered to be independent of each other. The data set was fairly small (maximum of 18 data points for each group) and not normally distributed, therefore non-parametric statistical methods were used (Siegel & Castellan, 1988). Tests were one-tailed where specific predictions were made, if not two tailed tests were undertaken, significance was set at a level of $p< 0.05$.

5.4 Results.

Results were examined according to the three measures recorded. Species were initially compared on the actual number of responses, the mean latencies to execute each of the responses, and were finally compared on the basis of the objects themselves.

5.4.1 Time to exit.

A Mann-Whitney U-Test failed to demonstrate any difference in time to exit between the 2 species ($U = 17.5, N_a = 7, N_b = 6$, Non-significant) and all individual groups had an average exit time of less than 30 seconds (Table 5. A).

Table 5.A : Mean latency in seconds to exit from indoor areas, during novel object trials (Results are based on 18 objects for each group).

Group	Mean	Standard error	Range	Group	Mean	Standard error	Range
SF1	4.0	1.0	1 - 13	SL1	5.4	1.2	1 - 18
SF2	3.7	0.6	1 - 8	SL2	19.4	11.3	1 - 208
SF3	22.7	8.2	1 - 148	SL3	33.4	7.8	3 - 135
SF4	22.4	10.6	1 - 190	SL4	1.9	0.3	1 - 5
SF5	5.2	1.0	1 - 15	SL5	2.0	0.3	1 - 6
SF6	5.4	1.3	1 - 21	SL6	3.8	0.9	1 - 16
SF7	3.9	0.5	1 - 8				
	9.6	3. 4	1- 190		11.0	5.2	1 - 208

The overall mean latency to exit for *S. labiatus* was 11.0 seconds (range 1-208 secs.), and for *S. fuscicollis* was 9.6 seconds (range 0-190 secs), and so all animals were usually quick to exit and consequently to view the object. Neither species was particularly more reluctant nor eager than the other to leave their indoor area, and so subsequent behaviour concerning the reaction to the novel object could not be merely due to differences in the latency to observe the objects.

5.4.2 Success : completed sessions by subjects.

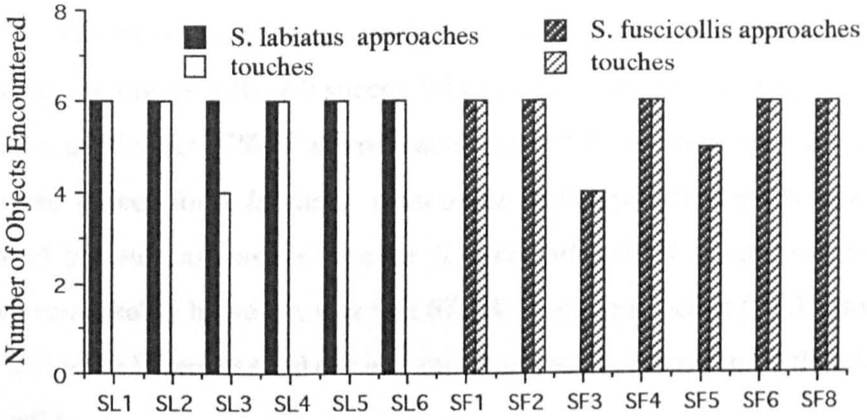
All subjects were presented with 6 sample sessions in each of the 3 areas, therefore for *S. labiatus* there was a potential of 36 completed session for each area, and 42 sessions for *S. fuscicollis*. A session was deemed successful if one or more of the individuals in the study group approached and touched the object. Immediately it was clear that there were individual differences intraspecifically in the the success rates, although species specific trends also occurred (Figure 5. A).

Both species behaved fairly similarly at the top area, although not all objects were touched. All of the *S. labiatus*, except SL3, approached and touched all of the objects (Figure 5.A[I]). In *S. fuscicollis*, on the other hand, 3 objects were neither approached nor touched. Specifically, five of the groups approached and touched all six objects, while SF5 approached and touched 5 objects and SF3 approached and touched only 4 objects. However, these differences were not significant, for either measure ($U = 15$ for Approach, $U = 19$ for Touch, $N_a = 7$, $N_b = 6$). In terms of objects presented in the middle area, all subjects approached and touched all objects, regardless of species, so the 2 species did not differ significantly ($U = 21$ for Approach, $U = 21$ for Touch ; $N_a = 7$, $N_b = 6$, both non-significant: Figure 5.A[II]).

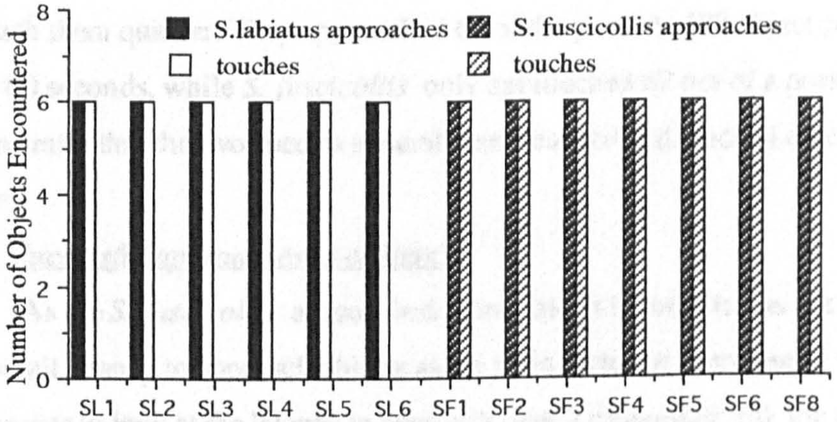
The only significant differences found between the species were when objects were placed on the floor of the cage. *S. fuscicollis* approached all but two of the objects (95%), while *S. labiatus* only approached 6 of the objects (17%). This was almost exactly repeated for the 'touching object' category, except that SL4 approached but did not touch one of the objects. Clearly these differences were significant ($U = 0$, $N_a = 7$, $N_b = 6$, $p < 0.01$) and striking in pattern (Figure 5.A[III]).

Overall success was different for the species, with *S. fuscicollis* touching every object that they approached, and demonstrating a higher success rate (121/ 126 ; 96%) than the *S. labiatus* (approaches 78/108 ; 72%, touches 75/108 ; 69%).The total number of successes was significantly greater for *S. fuscicollis* than *S. labiatus* ($U = 0$, $N_a = 7$, $N_b = 6$, $p < 0.01$).

I : Top area novel objects



II : Middle area novel objects



III : Floor area novel objects

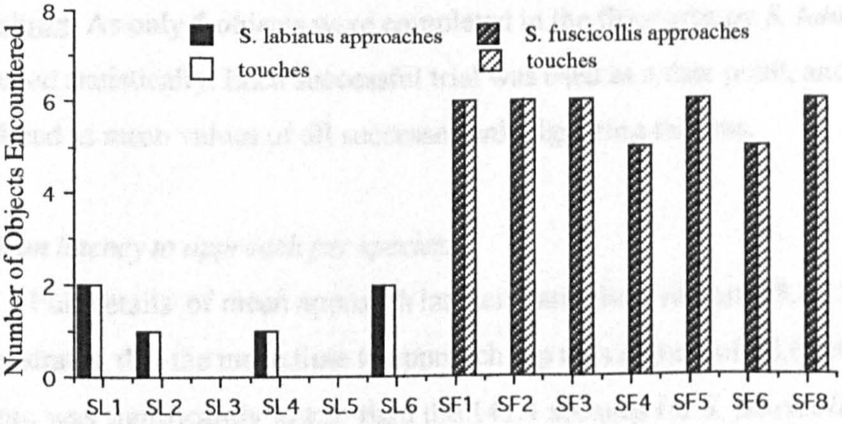


Figure 5.A : Total mumber of approaches and touches of novel objects, by two species of tamarins.

5.4.3 Latency to succeed.

The latency to approach, and consequently to touch, was usually very rapid for both species (see Figure 5.B). All successful trials were completed in under 20 minutes for both species, and in fact 97% of all approaches and 96% of touches were completed in under 10 minutes. Indeed for *S. labiatus* most of the total approaches and touches (both 97%) occurred under 5 minutes, as was the case for *S. fuscicollis*, (90% of approaches and 89% of touches). More remarkably however, was that 67.3% of all approaches (92.3% for *S. labiatus* ; 51.2% for *S. fuscicollis*) were carried out in 1 minute or less, as were more than half of the touches (54.6%).

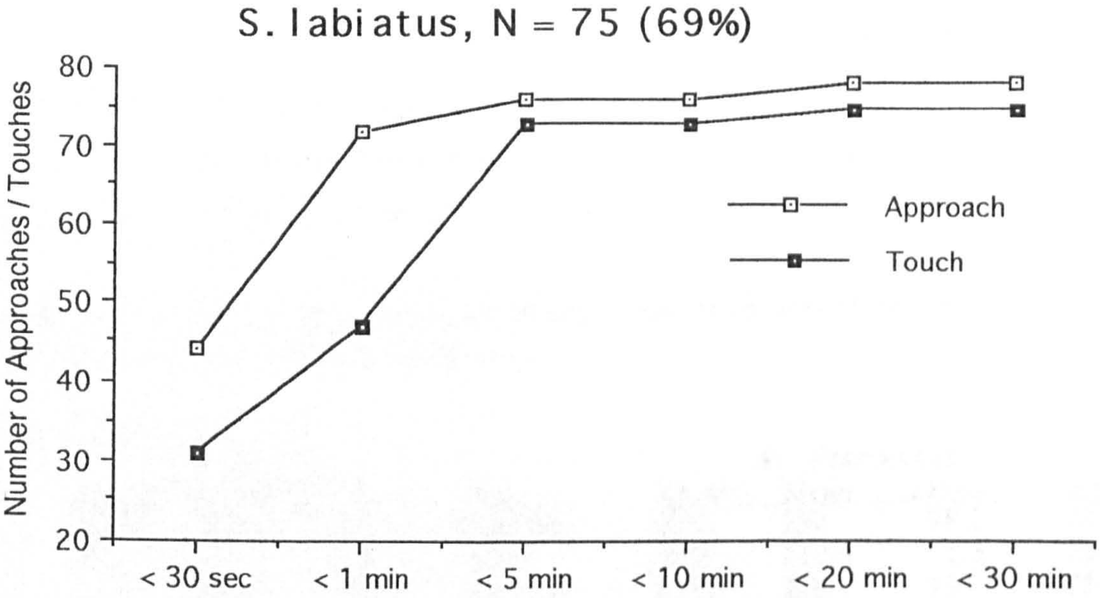
While *S. labiatus* approached less objects in total than the *S. fuscicollis*, they tended to approach them quicker. They approached 64 of the possible 108 object presentations (59%) in under 60 seconds, while *S. fuscicollis* only approached 62 out of a possible 126 (49%). This demonstrates that the two species generally approached and touched objects in a species distinct manner.

5.4.5 Successful approaches to objects.

As the *S. fuscicollis* approached more objects in total, it was not appropriate to compare the overall latency to approach objects as the main factor. A more useful way to compare the species was to look at the latency to approach over 2 categories; (a) the mean time to approach all objects in an area for each species, and (b) the mean time spent by each species to approach each object. As only 5 objects were completed in the floor area by *S. labiatus* , this area was not compared statistically. Each successful trial was used as a data point, and latencies were calculated as mean values of all successes only, ignoring failures.

(a) *Mean latency to approach per species.*

Full details of mean approach latencies are given in Table 5.B. Figure 5.C[I] demonstrates that the mean time to approach top area objects of 40.6 seconds per group of *S. labiatus*, was significantly lower than the 141.4 seconds for *S. fuscicollis*, even though both species approached most objects ($U = 2.5, N_a = 6, N_b = 7, p < 0.01$).



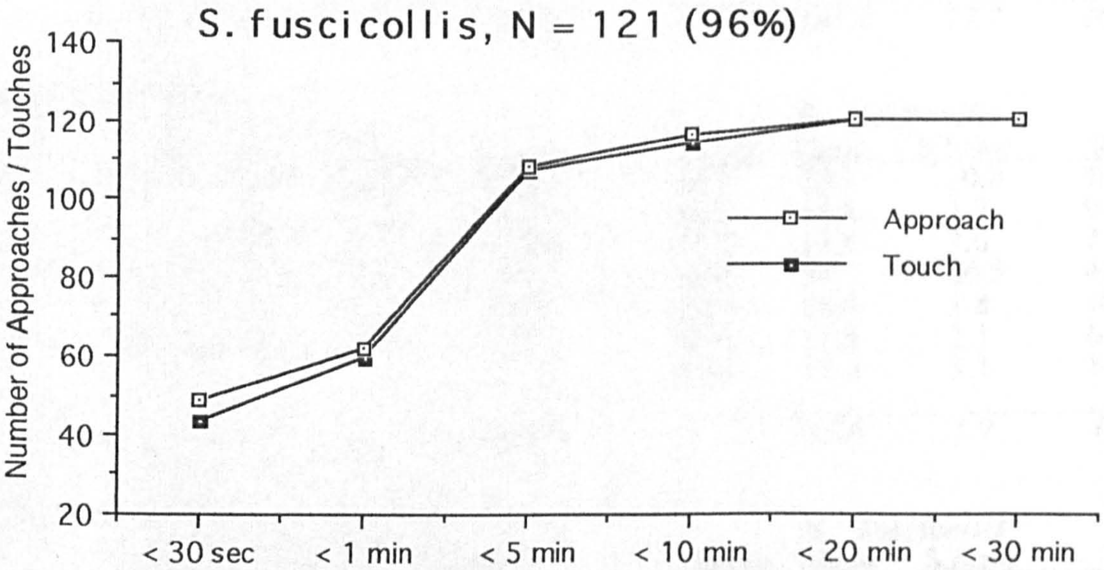


Figure 5.B : Cumulative number of approaches and touches of novel objects, where only completed trials (approached and touched) are used.

The mean approach time for middle area objects was almost identical for both the species, with *S. fuscicollis* having a mean approach time of 22.7 seconds and *S. labiatus* approaching in a mean time of 26.6 seconds (U = 17.5,N_a =6, N_b=7, non-significant). Table 5.B shows that the group means of middle area objects overlapped extensively. Finally, *S. labiatus* reacted to only 6 floor objects within the time period, and that *S. fuscicollis* reacted to 40 / 42 objects, so there is a quicker approach by the latter species.

Table 5. B : Mean approach latency per group, compared by area of object presentation. Means calculated from completed approaches only.

Top objects

S. labiatus

Group	Mean	S.Error	Range
SL1	45.0	13.4	13-108
SL2	51.5	10.7	9-80
SL3	81.5	27.7	35-214
SL4	19.7	4.0	6-32
SL5	22.5	8.5	10-63
SL6	23.3	3.9	15-42
Mean	*40.6*	*9.7*	*9-214*

S. fuscicollis

Group	Mean	S.Error	Range
SF1	159	98.2	24-647
SF2	112.5	21.3	28-167
SF3	224	114.1	25-552
SF4	239	78.5	30-497
SF5	144	66.3	10-315
SF6	59.5	21.5	14-146
SF8	51.5	18.6	12-136
	141.4	*27.7*	*10-647*

Middle objects

S. labiatus

Group	Mean	S.Error	Range
SL1	21.5	6.7	6-44
SL2	24.5	5.7	9-47
SL3	51.8	35.7	5-227
SL4	23.2	7.0	9-42
SL5	25	9.0	9-69
SL6	13.5	3.3	3-22
Mean	*26.6*	*5.3*	*3-227*

S. fuscicollis

Group	Mean	S.Error	Range
SF1	29.7	10.9	7-73
SF2	16.8	3.7	9-29
SF3	13.5	3.0	7-24
SF4	38	26.5	4-170
SF5	28.5	7.8	10-58
SF6	11.5	2.1	6-19
SF8	12.3	5.1	5-37
	22.8	*3.7*	*4-170*

Floor objects

S. labiatus

Group	Mean	S.Error	Range
SL1			
SL2			
SL3			
SL4			
SL5			
SL6			
Mean	*N/ A*		

S. fuscicollis

Group	Mean	S.Error	Range
SF1	225.8	36.7	102-377
SF2	115	23.4	47-204
SF3	298.8	142.4	26-949
SF4	176.8	176.8	13-953
SF5	223	95.1	41-631
SF6	138.2	44.6	62-288
SF8	143	38.7	47-258
	188.5	*24.3*	*10-953*

(b) *Mean latency to approach each object.*

Variations in the overall mean latencies for each group to approach may have been influenced by the objects used in each area, and so it was important to compare the response of both species to each individual object. A Binomial Sign Test (Coolican,1990) is appropriate, as it compares the relative values for each object condition.

Table 5.C : Mean latency to approach novel objects per species, compared over individual objects and areas (* Significant difference in Binomial Sign Test, $p = 0.05$).

TOP AREA

OBJECT	*S. labiatus*	*S. fuscicollis*
19	41.5	49.6
17	35.2	212.4
15	53.5	72.4
2	45	159.2
24	35.9	210.2
7	32.2	145
MEAN	*40.6 (SE 9.8)**	*141.40 (SE 27.7)**

MIDDLE AREA

OBJECT	*S. labiatus*	*S. fuscicollis*
3	24.4	24.9
22	48.9	40.8
23	12.8	11.8
6	10.2	12.2
18	29.9	12.9
12	33.5	32.9
MEAN	*26.6 (SE 5.3)*	*22.8 (SE 3.7)*

FLOOR AREA

OBJECT	*S. labiatus*	*S. fuscicollis*
9	N / A	84
11	N / A	246.7
4	N / A	97.1
10	N / A	122.7
20	N / A	347.7
21	N / A	239.2
MEAN		*250.8 (SE 55.7)*

The six top objects had a significantly quicker mean approach time for *S. labiatus* ($S = 0, N = 6, p = 0.05$), while the middle objects showed no significant difference between the species ($S = 2, N = 6$, Non-Significant). As *S. labiatus* only approached 3 of the floor objects it was not appropriate to compare the mean latency to approach objects in this area. All object means are shown in Table 5.C.

5.4.6 Successful touches of objects.

Since *S. fuscicollis* touched more objects, most of which were on the floor (the slowest completed area), it was not appropriate to compare the overall latency to touch objects. Again it was more useful to compare the species in 2 ways ; (a) the mean latency to touch all objects in an area for each species, and (b) the mean latency for each species to touch each object. Each successful trial was used as a data point, and latencies were calculated as mean values of all successes only, ignoring failures. Once again the floor area had too few touches by *S. labiatus* to compare the species statistically.

(a) *Mean latency to complete touches per group.*

All details of mean touch times are given in Table 5.D. Figure 5.C[I] demonstrates that the mean time to touch individual Top area objects of 87.7 seconds for *S. labiatus* was significantly lower than the 172.5 seconds for *S. fuscicollis*, even though both species eventually touched most objects ($U = 9$, $N_a = 6$, $N_b = 7$, $p < 0.01$).

S. fuscicollis had a lower mean time to touch middle area objects than *S. labiatus* (28.3 vs. 52.6 seconds) but this difference failed to reach significance ($U = 10$, $N_a = 6$, $N_b = 7$, non-significant). As S. fuscicollis reacted to 40 / 42 floor area objects and *S. labiatus* only touched 5/ 36, again there was no quantitative comparison to be made (Figure 5.C).

(b) *Mean latency to touch each object.*

Once again some variations in the latencies to touch may have been influenced by the objects used in each area, and it was deemed appropriate to compare the mean object touch time per species in a relative manner. Again, a Binomial Sign Test was appropriate as it compared the relative values for each object condition.

Table 5.D : Mean time to touch objects per group, compared by area of object presentation. Means calculated from completed touches only.

Top objects

S.labiatus

Group	Mean	S.Error	Range
SL1	65.3	19.5	18-154
SL2	86.8	15.5	46-151
SL3	264	96	68-528
SL4	35.8	9.6	15-74
SL5	47	12.8	22-99
SL6	27.2	4.2	17-46
Mean	*87.7*	*36.3*	*15-528*

S.fuscicollis

Group	Mean	S.Error	Range
SF1	161	97.8	24-647
SF2	114	21.7	28-171
SF3	343.8	230.5	25-1028
SF4	250.3	79.7	30-497
SF5	206	110.7	10-600
SF6	62.5	20.6	26-146
SF8	70	18.5	28-136
	172.5	*38.6*	*10-1028*

Middle objects

S.labiatus

Group	Mean	S.Error	Range
SL1	25.7	7.7	8-58
SL2	45.3	12.7	17-103
SL3	110.2	50.7	10-285
SL4	44.3	12.5	13-73
SL5	74.5	28	18-194
SL6	15.5	3.7	4-26
Mean	*52.6*	*14.2*	*4-285*

S.fuscicollis

Group	Mean	S.Error	Range
SF1	64.5	31.4	6-210
SF2	18.2	4.0	9-32
SF3	16.3	3.1	7-24
SF4	40.5	26	8-170
SF5	31.5	11.3	8-73
SF6	12.5	2.0	7-17
SF8	14.2	5.2	6-39
	28.2	*7.2*	*6-210*

Floor objects

S.labiatus

Group	Mean	S.Error	Range
SL1			
SL4			
SL3			
SL4			
SL5			
SL6			
Mean	*N / A*		

S.fuscicollis

Group	Mean	S.Error	Range
SF1	249.2	26.8	204-377
SF2	116.5	23.6	48-207
SF3	300.5	143.9	26-959
SF4	270	174	23-953
SF5	223	95.1	41-631
SF6	140	44	65-289
SF8	144	38.8	44-259
	206.2	*27.3*	*23-959*

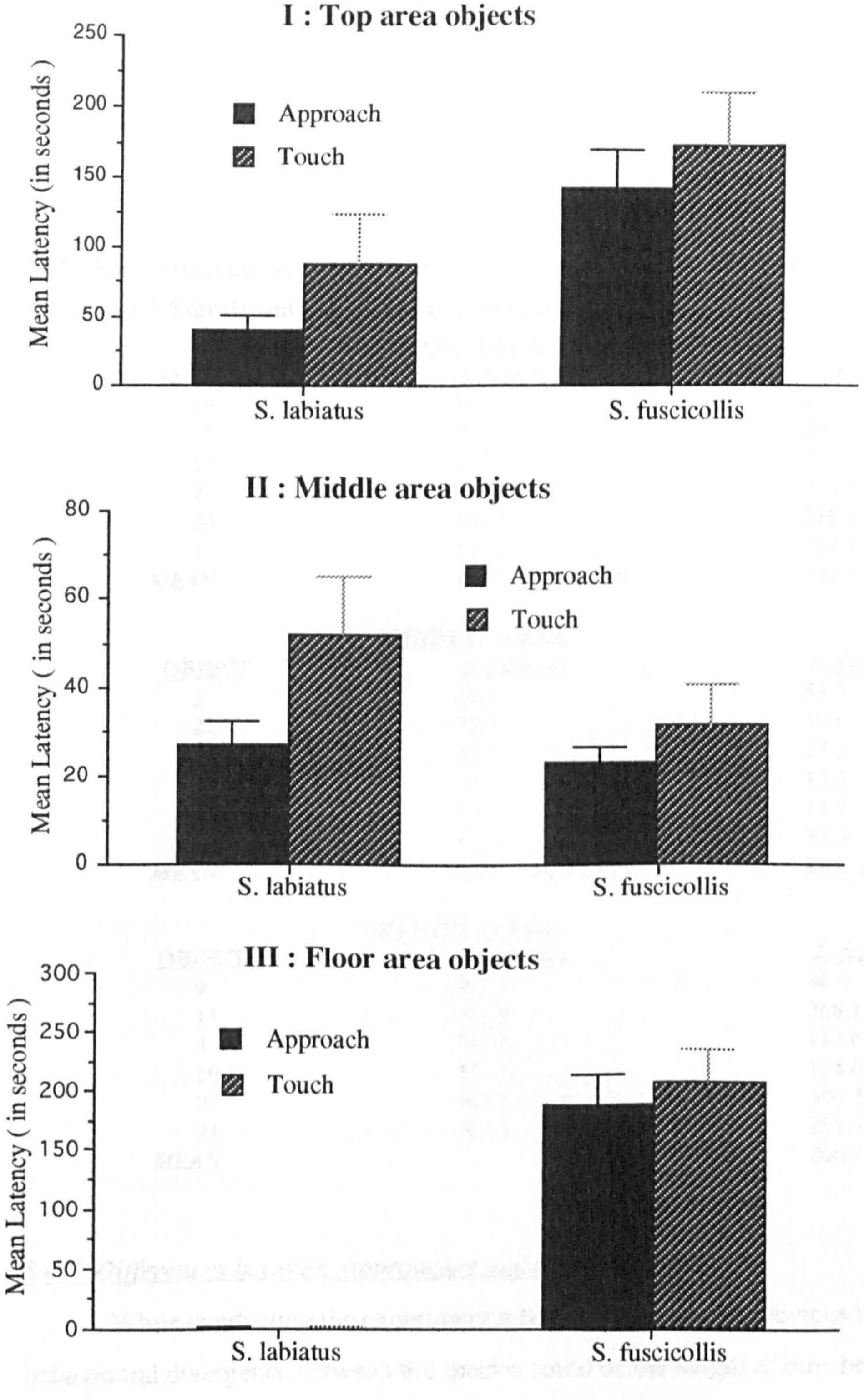


Figure 5.C : Mean latency to approach and touch novel objects for two tamarin species (N = 6 for *S.labiatus* and N = 7 for *S. fuscicollis*).

The six top objects had a significantly quicker mean time for *S. labiatus* to touch them (S =0, N = 6, p = 0.05), while the middle objects showed no significant difference between the species (S = 1, N = 6, Non-Significant), even though *S. fuscicollis* touched 5 of the 6 objects quicker. The mean time to touch per object, is shown in Table 5.E.

Table 5.E : Mean latency to touch novel objects per species, compared over individual objects and areas (* Significant difference in Binomial Sign Test, p = 0.05).

TOP AREA

OBJECT	*S. labiatus*	*S. fuscicollis*
19	59.7	69.9
17	56.4	290.1
15	66.7	73.6
2	89	236.1
24	125.3	216.4
7	127.2	157.1
MEAN	*87.7 (SE 36.3)**	*172.5 (SE 38.6)**

MIDDLE AREA

OBJECT	*S. labiatus*	*S. fuscicollis*
3	30.2	51.3
22	70.7	39.9
23	39.7	17.2
6	28	12.5
18	83.8	14.9
12	63.2	33.9
MEAN	*52.6 (SE 14.2)*	*28.2 (SE 7.2)*

FLOOR AREA

OBJECT	*S. labiatus*	*S. fuscicollis*
9	N / A	86.4
11	N / A	268.1
4	N / A	119.6
10	N / A	124.0
20	N / A	390.2
21	N / A	251.5
MEAN		*206.1 (SE 27.3)*

5.4.7 Differences between approaches and touches.

While conducting the experiment it became increasingly obvious that one possible behavioural divergence between the species could be the length of time between approaching and touching an object. The results are obviously influenced by the reluctance of *S. labiatus* to investigate objects placed onto the ground, and the lack of data points once again excludes analysis of this area.

Over all completed trials, there was a significantly lower mean touch - approach time for *S. fuscicollis.* This is reflected in the mean difference of 11.3 seconds for *S. fuscicollis* as opposed to the 31.2 seconds for *S. labiatus* ($U = 4, N_a = 6, N_b = 7, p < 0.01$). This was the case for both middle areas objects ($U = 6, N_a = 6, N_b = 7, p < 0.05$) and even for top area objects ($U = 5, N_a = 6, N_b = 7, p < 0.05$), which the *S. labiatus* approached and touched quicker overall. This demonstrates that *S. fuscicollis* touched objects relatively sooner after the initial approach. *S. labiatus* had a more distinctive approach phase and separate touch phase and this became apparent upon further examination of the data.

There were a large number of almost immediate approach and touches (≤1 second) differences for *S. fuscicollis* while very few occurred for *S. labiatus* (Figure 5.D). With the differences examined at 5 seconds or less, it is clear that the *S. fuscicollis* had completed most (86%) of their touches and that the *S. labiatus* had only completed a third of theirs. By 10 seconds, *S. labiatus* had only completed slightly more than half of their total touches, but *S. fuscicollis* had completed over 90% of theirs. These differences demonstrate that *S. labiatus* are more hesitant to touch novel objects they have approached, than the *S. fuscicollis* which approach and touch almost immediately once they have decided to investigate an object (Figure 5.E). These differences existed, even though *S. labiatus* approached and touched top area objects significantly quicker. The difference between the species is illustrated best in the middle area, where there was a quicker mean time to touch these objects by *S. fuscicollis,* even though both species had approached the objects in an almost identical time.

Data were analysed in terms of approach / touch ratios, where this measure indicates how soon a touch comes after an approach, the higher the value, the quicker a touch was, relative to an approach. A score of 1.0 equals an immediate touch, and the lower the score the longer the gap between measures. These ratios clearly show that *S.fuscicollis* significantly touched all objects relatively quicker after approach, ($U = 4, N_a = 6, N_b = 7, p < 0.05$). This was also the case for both middle areas objects ($U = 8, N_a = 6, N_b = 7, p < 0.05$) and even for top area objects ($U = 4, N_a = 6, N_b = 7, p < 0.05$). The middle area objects showed a similar pattern, and the overall ratio was 0.91 for *S. fuscicollis* and 0.48 for *S. labiatus.*

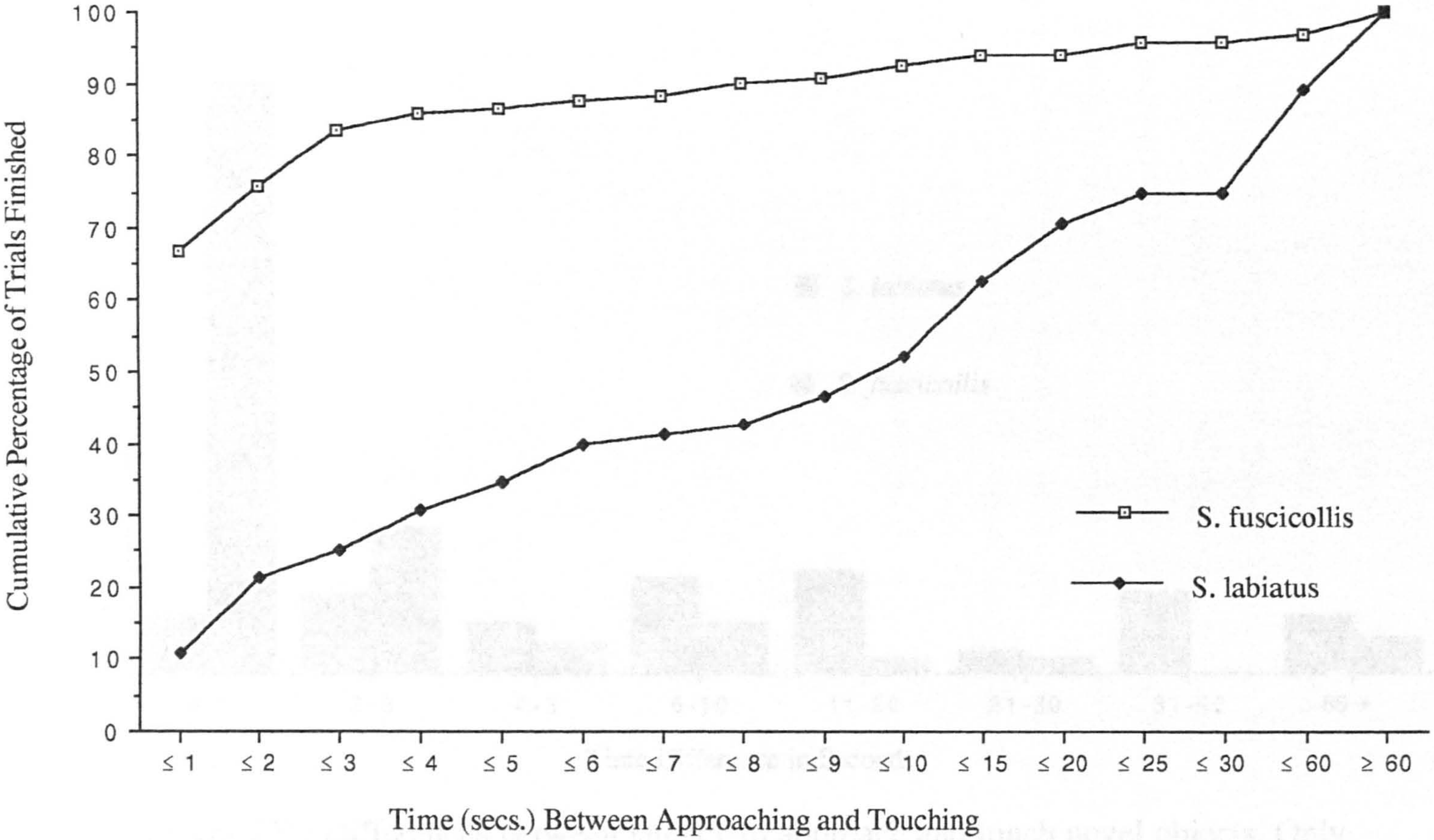


Figure 5.D : Differences between approaches and touches of novel objects. Expressed as cumulative percentages of completed trials over time.

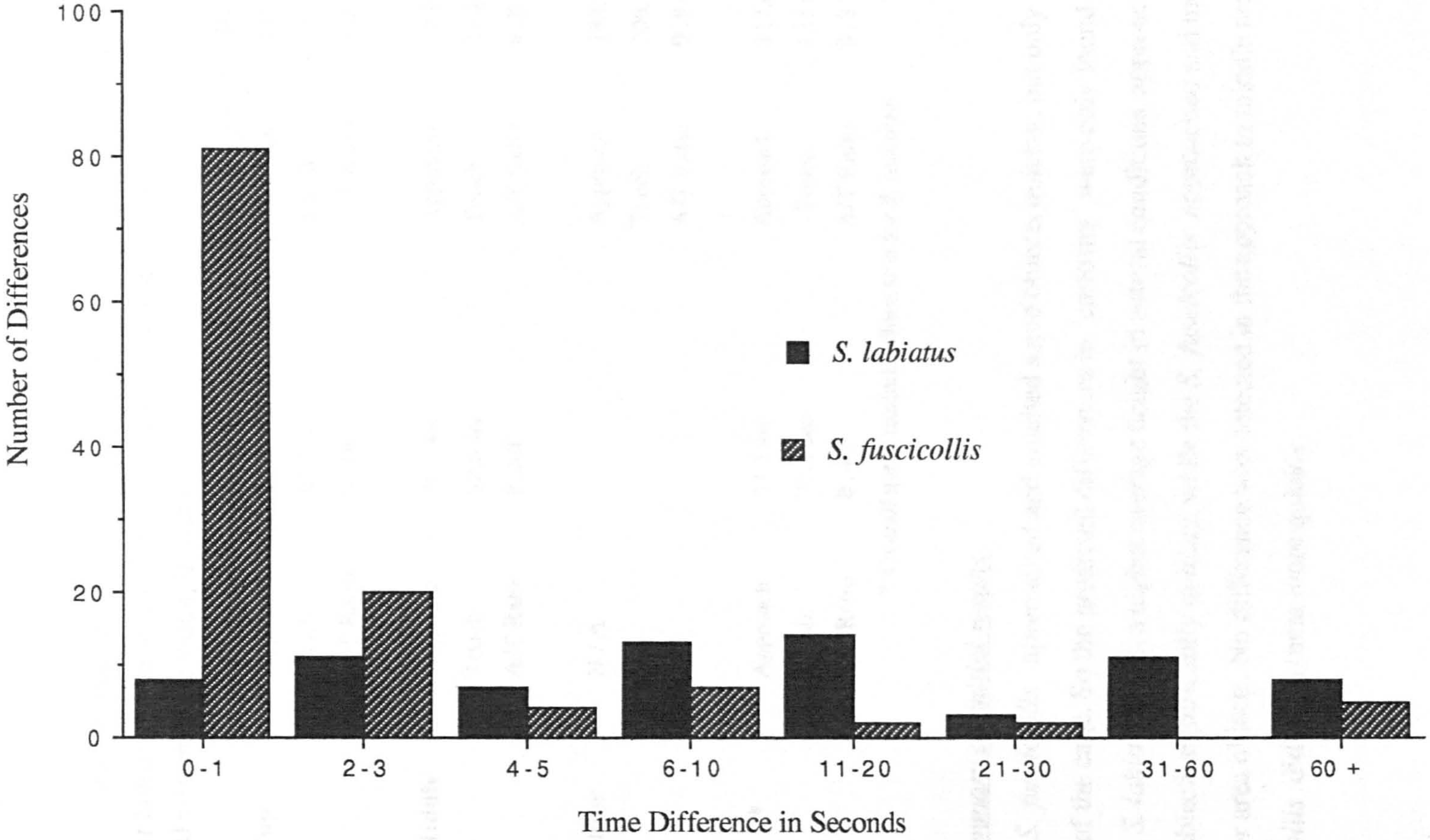


Figure 5.E : Differences between latency to approach and touch novel objects. Only completed trials are used (N = 121 for S.fuscicollis and N = 75 for S.labiatus).

This demonstrates that not only do the two species differ in the way they respond to objects in different areas, the species also differ in the overall method of responding.

Table 5.F Ratio of mean approach time and mean touch time for novel object trials in two species of tamarins. (Ratio for *S. labiatus* data in floor area is omitted due to low numbers). For Ratio, 1.0 = immediate touch, 0 = no touch

	S. labiatus		*S. fuscicollis*	
Top	Approach	40.6 sec	Approach	141.6 sec
	Touch	87.7 sec	Touch	172.5 sec
	A/T Ratio	**0.46**	A/T Ratio	**0.82**
Middle	Approach	26.6 sec	Approach	22.8 sec
	Touch	52.6 sec	Touch	28.2 sec
	A/T Ratio	**0.50**	A/T Ratio	**0.81**
Floor	N / A		Approach	188.5 sec
			Touch	206.2 sec
			A/T Ratio	**0.91**
All*	Approach	33.5 sec	Approach	117.6 sec
	Touch	70.2 sec	Touch	135.6 sec
	A/T Ratio	**0.48**	A/T Ratio	**0.87**

* Overall mean excludes floor area for *S. labiatus.*

<u>5.4.8 Summary of initial results.</u>

Overall, *S. fuscicollis* approached and touched some objects quicker, but only those placed on the floor of the cage. So the predicted differences in 'curiosity' were only found on the floor area. The *S. labiatus* with a higher average height in natural conditions, approached and touched top area objects significantly quicker, while the *S. fuscicollis* approached and touched many more floor area objects. No difference was detected in the approach to middle area objects, but *S. fuscicollis* did touch them more quickly.

5.5 Why do *S. labiatus* not go down to the floor objects ?

As the main differences between the species were found to occur in floor area objects, it was hypothesised that, amongst others, there may be three or four possible reasons for the failure to react.

(i) Physical Distance : there is a greater distance to travel from the exit of the indoor area to the floor, than for other conditions.

(ii) Danger : the animals may 'feel' more danger on the floor, than other areas.

(iii) Objects : are some characteristics of the objects used on the floor different to those objects used in the other areas ?.

(iv) Arboreality : *S. labiatus* is usually found higher up in its natural habitat (see Chapter 1) and this may account for differences.

While reasons (i) and (ii) are true, they were also the same for the *S. fuscicollis* and are justifiably not enough to explain any differences between the species. In terms of potential differences, the distance and danger elements are probably not enough to explain the large difference, but may explain why the *S. fuscicollis* took longer to complete this condition than the other areas. Arboreality is certainly a factor that could explain the results, and this has been proposed as a difference that may persist in captivity (see Chapters 1 & 4) and the evidence of the quicker response of *S. labiatus* to top area objects also supports this. There does however remain a strong possibility that the objects themselves had a large influence on the animals' behaviour. This was tested as a second phase of single species novel object trials, on *S. labiatus* only.

5.5.1 Method.

The six groups of *S. labiatus* were re-tested on some of the objects used in the novel object trials. Each group was re-tested on 3 objects from the floor (F) area that they had previously failed to touch, but this time the objects were placed in the middle (M) area of the cage (F-M). The main prediction was that if these objects themselves were not the cause of the prior failures, then they should be approached in this condition. A control presentation was also included in the experimental design where 3 previously approached objects from the middle area which were now placed on the Floor (M-F). Specifically the following points were tested ;

(a) Would the *S. labiatus* approach and touch objects that had been previously ignored when placed in the floor area, but are now placed in the middle ? (i.e. If the objects were not the cause for the lack of response, then they should be approached in the middle area).

(b) Would the *S. labiatus* approach previously investigated objects when placed in the floor area ? (i.e. M-F objects)

It was also decided that repeated presentations of previously used objects could potentially lead to habituation and therefore disinterest in an object. This could account for non-approach to the floor area, and in order to test this, another control condition was added, whereby the original middle area objects were again tested in the middle area (M-F-M). The main question examined here was would the subjects have become habituated to previously approached objects and so not be interested in approaching them ?.

Each group was tested in a similar way to the initial experiment (5.1A), but based on the timescale of successful approaches, it was decided that 20 minutes was sufficient time to wait for a response. The study was conducted some 2-3 weeks after the initial experiment. Each object was tested on a different, dry and mild day, with the order of middle and floor object presentations being varied. All 6 previously used floor objects were tested, as were all the middle area ones. The same 3 middle area objects that were now tested on the floor (M-F) were then re-tested for a third time but again in the middle area (M-F-M).

5.5.2 Results.

The initial results show that all 18 presentations of the F-M objects were now investigated and that only one of the M-F objects was now approached and touched (Table 5.G). These new middle area objects were now approached in a mean time of 23.5 seconds which was similar to the previous middle area overall mean approach time of 26.6 seconds. The *S. labiatus* were not as 'hesitant' as before, because the time to touch was much lower now and occurred sooner after the approach then for previous trials [Mean Touch - Approach time; **F-M** = 4.5 (SE 1.6) seconds, **Middle Objects** = 26.0 (SE 9.5)]. This difference was however non-significant (U = 7.5, N_a =6, N_b =6, Non-significant), but it does suggest that perhaps because the objects had been encountered (albeit only visually) they were not strictly "novel" and therefore the monkeys responded differently towards them, showing less hesitation to touch. This turned out not to be a significant factor, as the M-F-M control condition demonstrated (Table 5.H).

Table 5.G : Re-testing of floor objects previously not approached and touched, (now placed in middle Area; F-M) and successfully approached middle area objects now placed on floor (M-F). Latencies are in seconds.

		F - M			M - F	
Group	Object	Approach	Touch	Object	Approach	Touch
SL1	**4**	37	38	**22**	N/A	
	11	10	19	**3**	N/A	
	9	25	47	**6**	N/A	
SL2	**9**	5	12	**12**	N/A	
	20	25	29	**22**	N/A	
	10	6	14	**6**	N/A	
SL3	**21**	125	129	**23**	N/A	
	11	54	57	**3**	N/A	
	4	26	26	**18**	N/A	
SL4	**4**	14	17	**18**	N/A	
	20	16	18	**12**	N/A	
	10	21	22	**23**	N/A	
SL5	**20**	13	18	**22**	N/A	
	21	7	13	**3**	N/A	
	9	4	10	**12**	N/A	
SL6	**20**	12	12	**6**	84	86
	21	2	2	**22**	N/A	
	11	21	21	**12**	N/A	
Mean Value		**23.5**	**28.0**			
Standard Error		6.7	6.7			
Mean touch-approach			**4.5**			
Standard Error			1.6			

Table 5.H : Comparison of approach and touch times for original middle area objects and M-F-M novel object trials (Latencies are in seconds).

	Original			M - F - M		
Group	Object	Approach	Touch	Object	Approach	Touch
SL1	22	6	8	22	44	45
	3	16	19	3	8	9
	6	9	13	6	27	31
SL2	12	29	39	12	42	65
	22	15	55	22	9	30
	6	16	17	6	10	11
SL3	23	7	20	23	110	-
	3	50	72	3	24	25
	18	17	250	18	69	93
SL4	23	23	73	23	14	18
	12	48	66	12	26	33
	18	40	52	18	27	34
SL5	22	15	25	22	6	24
	3	20	22	3	53	55
	12	69	194	12	16	25
SL6	6	6	7	6	11	12
	22	20	26	22	59	61
	12	10	12	12	27	29
Mean Value		23.1	53.9		32.3	35.3
Standard Error		4.2	15.5		6.3	5.4
Mean Touch-Approach			30.7			7.5
Standard Error			13.8			2.0

The latency to approach and touch an object was compared using a Wilcoxon Signed Ranks Test (Siegel & Castellan,1988) as the same object was tested on the same groups in both conditions. The original mean approach time of 23.1 seconds was quicker than the mean M-F-M mean approach time of 32.3 seconds. However this was not a significant difference (T = 16, N = 6, non-significant), even though half of the M-F-M approaches were slower. The main difference appeared in the time to touch, where although the initial approach was quicker, the animals took longer to touch the objects. Again this difference was not significant (T = 16, N = 6, non-significant), even though the mean time to touch was only 35.3 seconds for the M-F-M presentation but was 53.9 seconds initially.

This suggests that the animals had been slower to approach, but were perhaps less intimidated, in the M-F-M presentation. However the mean difference between approach and touch over the two conditions was now found to be significant ($T = 21$, $N = 6$, $p<0.01$). This corresponds with the quicker touch shown towards M-F-M objects, although it is not clear whether the quicker touch time was due to repeated presentations, or was specifically due to a lack of "novelty" in re-used objects.

5.6 Experiment 5.1C : Novel objects presented to mixed-species groups.

5.6.1 Introduction.

In the single species condition (Section 5.4 , Experiment 5.1A), the two species were shown to differ in the way they reacted to the presentation of novel objects. Both species reacted in a way that could be predicted from their relative height in the forest. These differences were found in both approaches and touches of objects. The most startling result was that the *S. labiatus* almost entirely failed to react to objects placed on the floor, and subsequent testing demonstrated that this failure was not due to the nature of the objects themselves. The present captive situation allows a comparison that may not be possible in the wild ; the behaviour of groups of each species can be compared both when in single and mixed groups, and between species. This enables a comprehensive examination of behaviour in and out of association.

The divergent pattern of reaction to top and floor area objects, allows for a prediction to be made, involving the behavioural facilitation hypothesis. This hypothesis suggests that mixed-species groups allow the possibility of a facilitation of behavioural responses between the species and the opportunity for the congeners to benefit from the responsiveness of the other species (e.g. Gartlan & Struhsaker, 1972 ; see Chapter 1, and Section 5.1). In the present case, the reaction of one species approaching and touching a novel object, should allow a facilitated response in the congener. The following predictions could be made ;

1) The quicker average response of *S. labiatus* to top area objects should lead to a facilitated response by *S. fuscicollis* to these objects.

2) Similarly, the quicker average response of *S. fuscicollis* to floor area objects should also lead to a facilitation of the response by *S. labiatus* to these objects.

3) As both species responded almost identically to middle area objects, there should be no significant difference in response to objects in this area.

These predictions were tested on mixed-species groups.

5.7 Methods.

5.7.1 Subjects.

Mixed groups, formed from five pairs of each species (GP3 : SL1 & SF3; GP4 : SL2 & SF5; GP6 : SL4 & SF8; GP7 : SL3 & SF6; GP8 : SL6 & SF2) were tested during this experiment. Each mixed- species group was housed in a separated double indoor / outdoor cage system, and all mixed groups were separated from each other by at least one adjacent cage, containing a different species of callitrichids (see Chapter 3 for details). Testing was carried out during June & July 1994.

5.7.2 General procedure.

The procedure was identical to that used for Experiment 5.1.A, and each mixed-species group was tested, on the same set of new objects (see appendix 2), and in exactly the same way as the monospecific trials. The only difference was that the behaviour of the two species was noted concurrently during the same trial, (i.e. the latency to exit, time to approach (<15cm) and to touch the object, was recorded for the first member of each species).

5.8 Results.

5.8.1 Analysis of Experiment 5.1C.

The results were initially compared between the species, for the mixed group condition (Section 5.8), and were then compared within species, between the conditions (Section 5.9) with the results examined to investigate any general differences between conditions.

5.8.2 Time to exit.

The two species were very similar in their mean latency to exit, with *S. fuscicollis* having a slightly faster mean exit time (9.0 seconds, Standard error 1.8) than *S. labiatus* (8.5 seconds, St. error 2.9). However, this was not significantly different ($U=10$, $N_a=5$, $N_b=5$, non-significant), and both species therefore left their indoor areas after a relatively short delay. These times were very similar to the mean exit times in the monospecific trials (*S. labiatus* 11sec : *S. fuscicollis* 9.6), and as a result were not significantly different ($U=8$, $N_a=5$, $N_b=5$, non-significant).

5.8.3 Approaches to objects in mixed-species groups.

Both species approached most objects, with an overall success rate for each species of over 95% (96.7% for *S. labiatus* ; 95.6% for *S. fuscicollis*). Once again failure was centred around a pattern ; specifically *S. fuscicollis* had 4 failures in the top area, while *S. labiatus* had 3 failures in the floor area. However, neither species was significantly more successful in any of the three areas (U=5 for top, U=12.5 for middle, U= 7.5 for floor, N_a=5, N_b=5, non-significant). The fact that *S. labiatus* now showed a 90% approach rate when part of mixed-species groups, is in stark contrast to the position when in single species groups, where only 17% of objects were approached.

The two species differed in their mean approach times per area, and the pattern was as predicted (Table 5.I). Overall, *S. fuscicollis* had a quicker mean approach time, but this was not significantly quicker (U=10, N_a=5, N_b=5, non-significant). The *S. labiatus* had a faster mean approach (26.5 sec) to top area objects than *S. fuscicollis* (77.31sec), and this was significantly quicker (U=0, N_a=5, N_b=5, $p<0.01$). Both species had a similar mean approach time to middle area objects (U=10, N_a=5, N_b=5,non-significant), while *S. fuscicollis* had a significantly quicker mean approach to floor objects (U=0, N_a=5, N_b=5, $p<0.01$).

5.8.4 Touches of objects in mixed-species groups.

Both species also touched all objects that they approached, so overall success was the same as that for approaches. There was an identical pattern of failure and once again, neither species was significantly more successful in any of the three areas (U=5 for top, U=12.5 for middle, U= 7.5 for floor, N_a=5, N_b=5, non-significant).

There was a difference in mean touch times per area, and the pattern was as predicted (Table 5.J). The *S. labiatus* touched top area objects significantly quicker (U=0, N_a=5, N_b=5, $p<0.01$), while conversely *S. fuscicollis* touched floor objects more quickly (U=0, N_a=5, N_b=5, $p<0.01$). Both species had a similar mean touch time for middle area objects (U=8, N_a=5, N_b=5, non-significant). Overall, *S. fuscicollis* had a quicker mean touch time, but this was not significantly quicker (U=9, N_a=5, N_b=5, non-significant).

Table 5. I : Mean latency to approach novel objects presented to mixed-species groups.

Top Objects

	S. labiatus			*S. fuscicollis*		
Group	Mean	S.Error	Range	Mean	S.Error	Range
GP3	14	4.0	5-28	66.4	22.1	22-149
GP4	26.8	6.3	9-45	64.5	26.0	17-131
GP6	30.7	11.0	11-84	93	22	37-169
GP7	53	12.1	15-102	108.7	41.5	32-269
GP8	8	1.8	2-14	54	20.5	16-136
Mean	***26.5***	***7.8***	***9-214***	***77.8***	***10.1***	***13-269***

Mann-Whitney, U =0, N_a =5, N_b =5, p<0.01

Middle Objects

	S. labiatus			*S. fuscicollis*		
Group	Mean	S.Error	Range	Mean	S.Error	Range
GP3	11.0	2.9	3-21	18.3	5.5	2-42
GP4	26.2	7.8	6-47	12.2	2.6	7-23
GP6	9.0	4.3	2-29	19.3	9.8	3-65
GP7	16.5	4.5	5-36	17.5	7.4	6-54
GP8	11.0	1.3	7-15	5.3	1.3	1-10
Mean	***14.7***	***3.1***	***2-47***	***14.5***	***2.6***	***1-65***

Mann-Whitney, U =10, N_a =5, N_b =5, non-significant

Floor Objects

	S. labiatus			*S. fuscicollis*		
Group	Mean	S.Error	Range	Mean	S.Error	Range
GP3	237.8	77.6	60-567	73.3	23.7	26-169
GP4	138.8	34.8	81-309	41	6.2	12-57
GP6	91.8	16.4	41-143	53.2	10.9	20-99
GP7	285.3	49.6	179-380	89	21.6	40-170
GP8	90.8	28.4	45-200	73.2	31.8	20-212
Mean	***168.9***	***39.5***	***41-567***	***65.9***	***8.4***	***12-212***

Mann-Whitney, U =0, N_a =5, N_b =5, p<0.01

Table 5. J : Mean latency to touch novel objects presented to mixed-species groups.

Top Objects

	S. labiatus			*S. fuscicollis*		
Group	Mean	S.Error	Range	Mean	S.Error	Range
GP3	17.2	3.8	5-29	68	22.4	23-152
GP4	29.5	6.2	12-47	65.5	26.0	18-132
GP6	34.2	11.9	13-92	94	22	38-170
GP7	54.5	12.1	16-103	110	41.6	14-270
GP8	9	1.9	3-16	54.8	20.4	17-136
Mean	***28.9***	***7.8***	***3-103***	***78.5***	***10.2***	***14-270***

Mann-Whitney, $U=0$, $N_a=5$, $N_b=5$, $p<0.01$

Middle Objects

	S. labiatus			*S. fuscicollis*		
Group	Mean	S.Error	Range	Mean	S.Error	Range
GP3	12.3	2.9	5-23	19.2	5.5	3-43
GP4	27.2	8.0	7-48	13.0	2.7	8-24
GP6	12.7	7.0	3-47	20.0	9.9	4-66
GP7	19	4.5	6-37	18.3	7.4	6-55
GP8	12.7	1.3	11-16	6.2	1.2	2-10
Mean	***16.7***	***2.9***	***3-48***	***15.3***	***2.6***	***2-66***

Mann-Whitney, $U=8$, $N_a=5$, $N_b=5$, non-significant

Floor Objects

	S. labiatus			*S. fuscicollis*		
Group	Mean	S.Error	Range	Mean	S.Error	Range
GP3	245.2	78.2	68-579	74.3	20.8	27-170
GP4	145.5	36.7	83-326	42.2	6.2	13-58
GP6	106.5	15.7	61-148	54.2	10.6	22-94
GP7	294.3	50.7	187-391	90.3	21.6	41-172
GP8	97.2	28.4	46-215	74.3	31.5	21-212
Mean	***177.7***	***39.2***	***46-579***	***65.9***	***8.5***	***13-212***

Mann-Whitney, $U=0$, $N_a=5$, $N_b=5$, $p<0.01$

5.8.5 Difference between approaching and touching in mixed-species groups.

S. labiatus had a mean difference between approaching and touching objects of 4.4 seconds, while *S. fuscicollis* had a mean difference of 1.0 seconds. These overall means were different (U=0, N_a=5, N_b=5, p<0.01), as were each of the three object presentations (middle and floor objects U= 0, N_a=5, N_b=5, p<0.01; top area objects U=4, N_a=5, N_b=5, p<0.05). This difference was mainly due to the almost immediate touch by *S. fuscicollis*, after initial approach (Figure 5.F). *S. labiatus* had a more distinct pause between initial approach and touch. Finally, this is once again clearly shown by the mean approach and touch ratios (Table 5. K). In all conditions the ratio is larger for *S. fuscicollis*, but overall there is little difference in scores. This is in contrast with the single species condition, where the *S. fuscicollis* had a much higher value of ratio than *S. labiatus.*

Table 5. K : Ratio of mean approach time and mean touch time for novel object trials in two species of tamarins. For ratio, 1.0 = immediate touch, 0 = no touch

	S. labiatus		*S. fuscicollis*	
Top	Approach	26.5 sec	Approach	77.3 sec
	Touch	28.9 sec	Touch	78.5 sec
	A/T Ratio	**0.92**	A/T Ratio	**0.98**
Middle	Approach	14.7 sec	Approach	14.5 sec
	Touch	16.7 sec	Touch	15.3 sec
	A/T Ratio	**0.88**	A/T Ratio	**0.95**
Floor	Approach	168.9 sec	Approach	66.0 sec
	Touch	177.7 se	Touch	67.1 sec
	A/T Ratio	**0.95**	A/T Ratio	**0.98**
All	Approach	65.2 sec	Approach	51.4 sec
	Touch	69.5 sec	Touch	52.4 sec
	A/T Ratio	**0.94**	A/T Ratio	**0.98**

5.8.6 Relative order of approaching and touching.

The species order of approaching and touching was compared within mixed groups (Table 5.L). Overall, the two species were not significantly different in the number of approaches and touches they were first to make (U=5.5, N_a=5, N_b=5, non-significant), even though *S. fuscicollis* were first to react to 59% (53/90) of objects. Significant differences were found in the top and floor areas.

In the top area, *S. labiatus* reacted to 83% (25/30) of objects before *S. fuscicollis* (U=0.5, N_a=5, N_b=5, p<0.01). In the floor area, the opposite pattern was found, where *S. fuscicollis* reacted first to 97% (29/30) of objects, which was significantly more than *S. labiatus* (U=0, N_a=5, N_b=5, p<0.01).

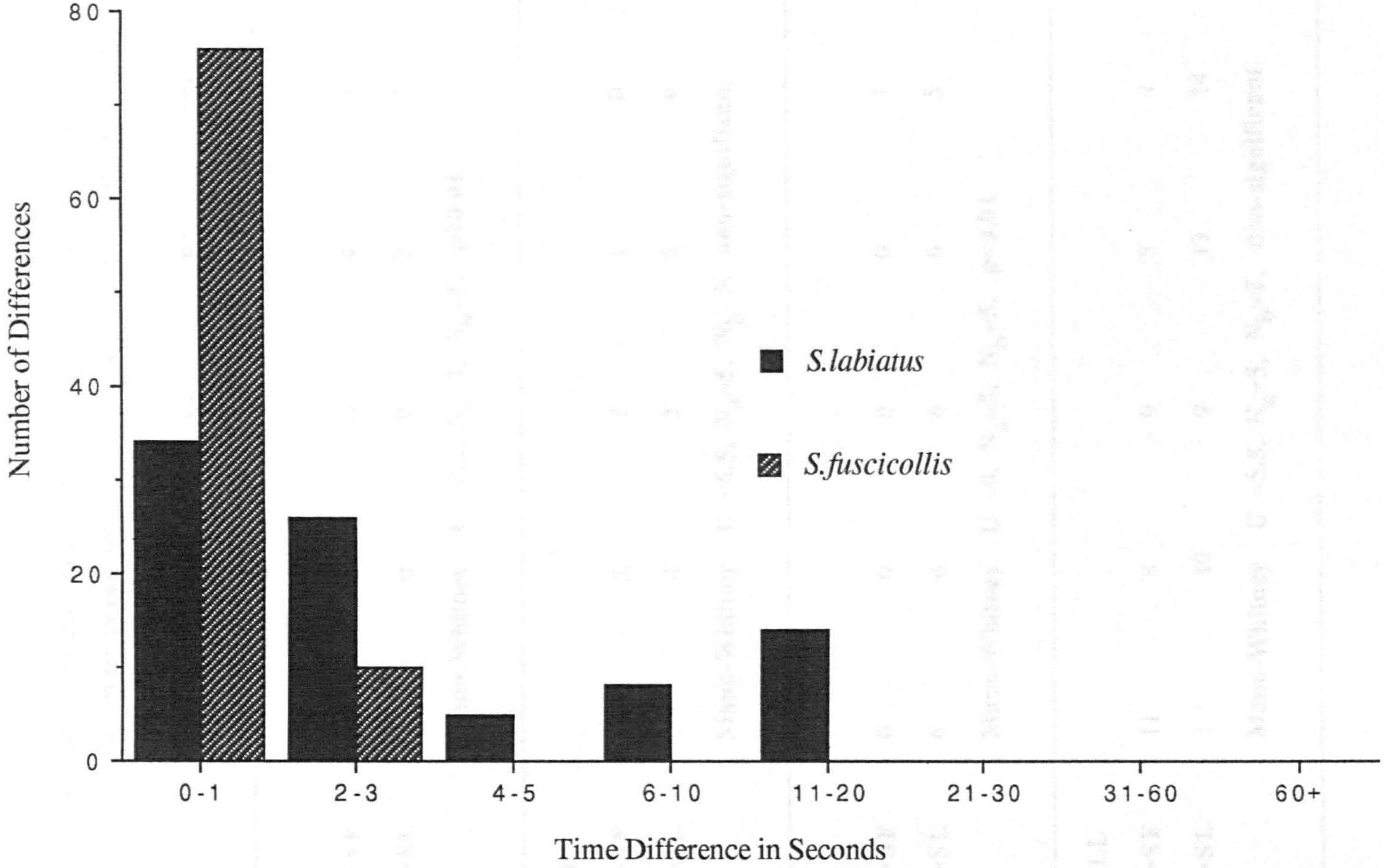


Figure 5.F : Difference between approach and touch, in mixed-species groups.

Finally, no significant differences were found in the middle area ($U=6.5$, $N_a=5$, $N_b=5$, non-significant), even though *S. fuscicollis* reacted first to 63% (19/30) of objects.

Table 5.L : Order of initial approaches and touches of novel objects, during mixed-species trials (For each group, N = 6 trials per area : SL = *S.labiatus*, SF = *S.fuscicollis*).

	GP3	GP4	GP6	GP7	GP8	TOTAL
TOP						
SL>SF	6	6	6	4	3	**25**
SF>SL	0	0	0	2	3	**5**
	Mann-Whitney U =0.5, N_a=5, N_b=5, $p<0.01$					
MIDDLE						
SL>SF	5	2	3	1	0	**11**
SF>SL	1	4	3	5	6	**19**
	Mann-Whitney U =6.5, N_a=5, N_b=5, non-significant					
FLOOR						
SL>SF	0	0	0	0	1	**1**
SF>SL	6	6	6	6	5	**29**
	Mann-Whitney U =0, N_a=5, N_b=5, $p<0.01$					
OVERALL						
SL>SF	11	8	9	5	4	**37**
SF>SL	7	10	9	13	14	**53**
	Mann-Whitney U =5.5, N_a=5, N_b=5, non-significant					

5.8.7 Summary of behaviour in mixed-species conditions.

S. labiatus were first to approach and touch top area objects, and they did so significantly quicker than *S. fuscicollis* (Table 5.M). The two species were not significantly different in their reaction to middle area objects. *S. fuscicollis* were first to react to floor area objects, doing so significantly quicker than their congeners. Overall, there were no significant differences, although the *S. fuscicollis* reacted more quickly and were first to react to more objects. In all areas, and overall, *S. fuscicollis* had a significantly shorter mean approach-touch difference, indicating a less "cautious" approach than *S. labiatus*.

Table 5.M : Summary of significant differences during mixed-species trials. (√SF = *S. fuscicollis* significantly different, √SL = *S. labiatus* significantly different, X = not significantly different).

	Approach Latency[1]	Touch Latency	App-Touch Difference[2]	Number of Successes[3]	First to App. & Touch[4]
TOP	√SL	√SL	√SF	X	√SL
MIDDLE	X	X	√SF	X	X
FLOOR	√SF	√SF	√SF	X	√SF
ALL	X	X	√SF	X	X

Comparisons :
[1] Fastest mean latency to complete objects.
[2] Smallest mean difference between measures.
[3] Largest mean number of completed objects.
[4] Greatest number of initial approaches and touches of objects.

5.9 Differences between single and mixed-species conditions.

5.9.1 Differences between latency to approach and touch.

For each species, the overall mean latency to both approach and touch, was less in mixed-species presentations (Table 5.N). However, the only significant difference was for touch in *S. labiatus* (T=15, N=5, p<0.05). Looking at individual differences between the conditions, by area, it is clear that both species approached and touched objects quicker when in mixed groups (Tables 5.O & 5.P). Unfortunately, few of these differences were significant (Figure 5.G).

Table 5.N : Overall mean latency to approach and touch novel objects, in single and mixed-species groups.

Approach

S. labiatus	**Single***	35.6	(St. error 6.7)
	Mixed	20.6	(St. error 4.4)
	Wilcoxon , T=12, N=5, non-significant		
S. fuscicollis	**Single**	106.1	(St. error 23.4)
	Mixed	51.4	(St. error 5.9)
	Wilcoxon , T=14, N=5, non-significant		

Touch

S. labiatus	**Single***	72.1	(St. error 23.4)
	Mixed	22.8	(St. error 4.4)
	Wilcoxon , T=15, N=5, p<0.05		
S. fuscicollis	**Single**	120.9	(St. error 27.5)
	Mixed	52.4	(St. error 6.0)
	Wilcoxon , T=14, N=5, non-significant		

(* *S. labiatus* in single species avoided floor area, so mean values for this condition are calculated from top & middle areas only)

Table 5.O : Mean latency to approach novel objects by members of 5 mixed-species groups, when tested in both single and mixed groups. Scores are reported as mean latency (in seconds) per session.

S. labiatus

	Top		Middle		Floor	
Group[1]	S	*M*	S	*M*	S	*M*
GP3 (SL1)	45	*14*	21.5	*11.0*	N/A[2]	*237.8*
GP4 (SL2)	51.5	*26.8*	24.5	*26.2*		*138.8*
GP6 (SL4)	19.7	*30.7*	23.2	*9.0*		*91.8*
GP7 (SL3)	81.5	*53*	51.8	*16.5*		*285.3*
GP8 (SL6)	23.3	*8*	13.5	*11.0*		*90.8*
Mean	44.2	*26.5*	26.9	*14.7*		*168.9*
St. error	11.1	*7.8*	6.5	*3.1*		*39.5*
T[3]	14		14			
Sig.[4]	N/S		N/S			

S. fuscicollis

	Top		Middle		Floor	
Group[1]	S	*M*	S	*M*	S	*M*
GP3 (SF3)	224	*66.4*	13.5	*18.3*	298.8	*73.3*
GP4 (SF5)	144	*64.5*	28.5	*12.2*	223	*41*
GP6 (SF8)	51.5	*93*	12.3	*19.3*	143	*53.2*
GP7 (SF6)	59.5	*108.7*	11.5	*17.5*	138.2	*89*
GP8 (SF2)	112.5	*54*	16.8	*5.3*	115	*73.2*
Mean	118.5	*77.8*	16.5	*14.5*	183.5	*65.9*
St. error	51.5	*10.1*	3.1	*2.6*	34	*8.4*
T[3]	12		9		15	
Sig.[4]	N/S		N/S		$p<0.05$	

[1] S = Scores when within single species groups

M = Scores when within mixed species groups

[2] Mean latency to approach objects, for successful trials only,

N/A = not enough successful trials to calculate means.

[3] Wilcoxon, T Statistic. [4] Probability of test.

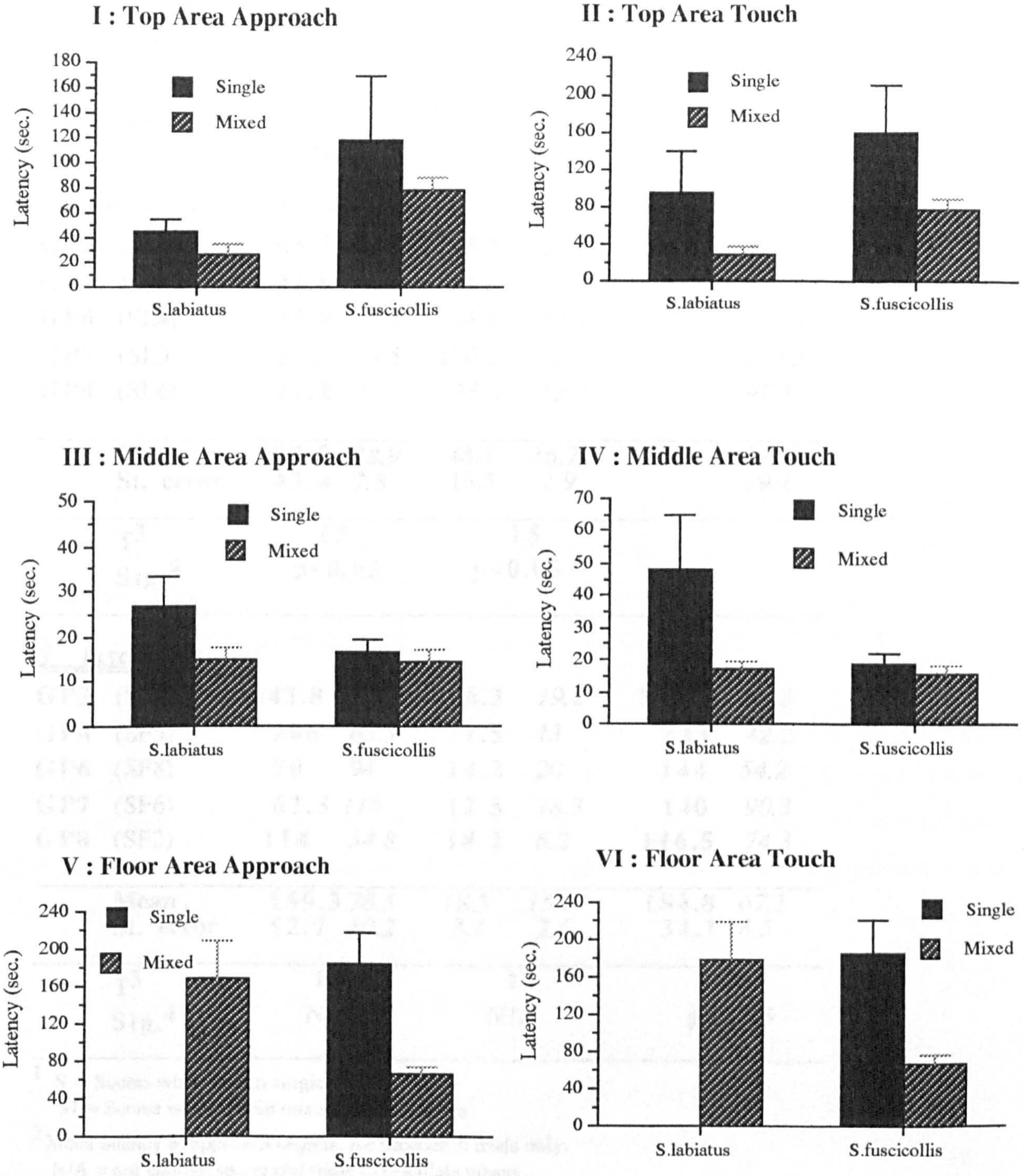


Figure 5.G : A comparison between mean approach and touch time, shown towards novel objects in single and mixed-species groups.

Table 5.P : Mean latency to touch novel objects by members of 5 mixed-species groups, when tested in both single and mixed Groups. Scores are reported as mean latency (in seconds) per session.

S. labiatus

	Top		Middle		Floor	
Group^1	**S**	***M***	**S**	***M***	**S**	***M***
GP3 (SL1)	**65.3**	*17.2*	25.7	*12.3*	N/A^2	*245.2*
GP4 (SL2)	**86.8**	*29.5*	45.3	*27.2*		*145.5*
GP6 (SL4)	**35.8**	*34.2*	**44.3**	*12.7*		*106.5*
GP7 (SL3)	**264**	*54.5*	**110.2**	*19*		*294.3*
GP8 (SL6)	**27.2**	*9*	**15.5**	*12.7*		*97.2*
Mean	**95.8**	*28.9*	**48.2**	*16.7*		*177.7*
St. error	**43.4**	*7.8*	**16.5**	*2.9*		*39.2*
T^3	**15**		**15**			
Sig.^{4}	**p<0.05**		**p<0.05**			

S. fuscicollis

	Top		Middle		Floor	
Group^1	**S**	***M***	**S**	***M***	**S**	***M***
GP3 (SF3)	**243.8**	*68*	**16.3**	*19.2*	**300.5**	*74.3*
GP4 (SF5)	**206**	*65.5*	**31.5**	*13*	**223**	*42.2*
GP6 (SF8)	**70**	*94*	**14.2**	*20*	**144**	*54.2*
GP7 (SF6)	**62.5**	*110*	**12.5**	*18.3*	**140**	*90.3*
GP8 (SF2)	**114**	*54.8*	**18.2**	*6.2*	**116.5**	*74.3*
Mean	**159.3**	*78.5*	**18.5**	*15.3*	**184.8**	*67.1*
St. error	**52.7**	*10.2*	**3.4**	*2.6*	**34.1**	*8.5*
T^3	**12**		**11**		**15**	
Sig.^{4}	**N/S**		**N/S**		**p<0.05**	

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[1] S = Scores when within single species groups
M = Scores when within mixed species groups

[2] Mean latency to approach objects, for successful trials only,
N/A = not enough successful trials to calculate means.

[3] Wilcoxon, T Statistic. [4] Probability of test.

Top area objects : Both species showed an improved response to top area objects, but neither approached them significantly quicker (*S. labiatus* T=14, *S. fuscicollis* T=12, N=5, non-significant). On the other hand, *S. labiatus* touched these objects significantly quicker (T=15, N=5, $p<0.05$), and although *S. fuscicollis* had an improved touch time, this failed to reach significance (T=12. N=5, non-significant).

Middle area objects : In mixed groups there was a non-significant decrease in mean latency to approach middle area objects for both *S. labiatus* (T=14, N=5, non-significant) and *S. fuscicollis* (T=9, N=5, non-significant). Once again *S. labiatus* showed a significantly quicker mean time to touch these objects (T=15, N=5, $p<0.05$), while *S. fuscicollis* had a non-significant increase (T=11, N=5, non-significant).

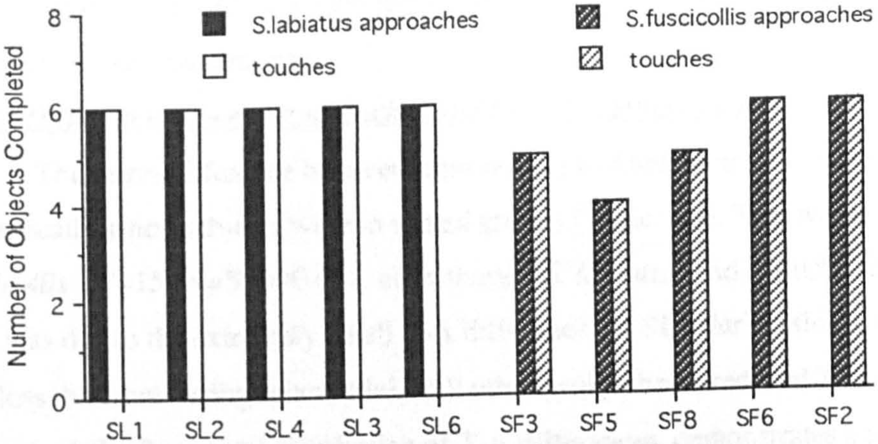
Floor area objects : These objects produced a problem for analysis, as *S. labiatus* did not approach or touch over 90% of objects in the single species groups. Therefore, the mean latency to approach and touch could not be directly compared between conditions. The two presentations are, however, compared in terms of overall success (Section 5.9.2). The *S. fuscicollis* had a significantly quicker approach and touch of floor area objects (T=15, N=5, $p<0.05$).

5.9.2 Differences in success between trials.

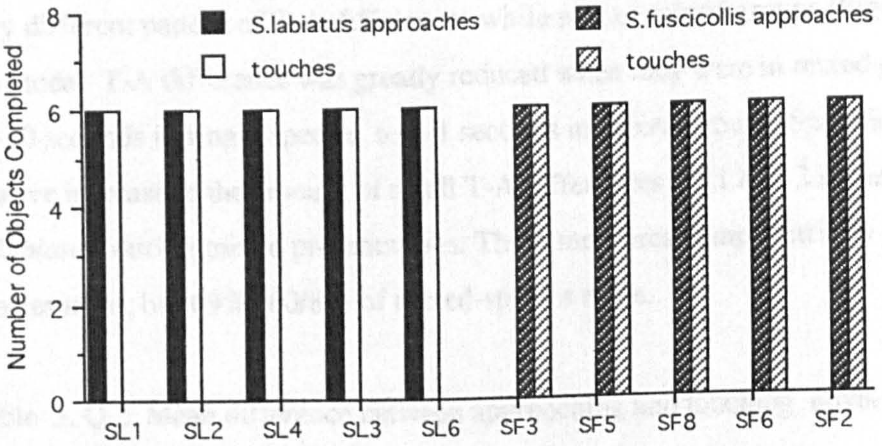
The main differences were concentrated on *S. labiatus*, as *S. fuscicollis* did not have any significant differences in success between conditions (Figure 5.H). The difference was that *S. labiatus* now approached and touched most of the floor area objects, completing 90% (27/30) of objects in mixed groups, compared to only 13% (3/30) in single groups. These differences were significant for both approach and touch (U= 0, N_a=5, N_b=5, $p<0.01$). As a consequence, there was now a significantly greater overall number of successes for *S. labiatus* (U= 0, N_a=5, N_b=5, $p<0.01$), but not for *S. fuscicollis* (U=12.5, N_a=5, N_b=5, non-significant).

Both species had a similar number of successfully completed trials of middle area objects (U=12.5, N_a=5, N_b=5, non-significant), where all objects were completed by each species in the two conditions. In the top area, a similar pattern was found for *S. fuscicollis,* which approached and touched a similar number of objects in both single and mixed groups (U=12.5, N_a=5, N_b=5, non-significant). *S. labiatus* approached and touched two more objects in mixed groups, but this was not a significant difference (U=10, N_a=5, N_b=5, non-significant).

A : Top area novel objects



B : Middle area novel objects



C: Floor area objects

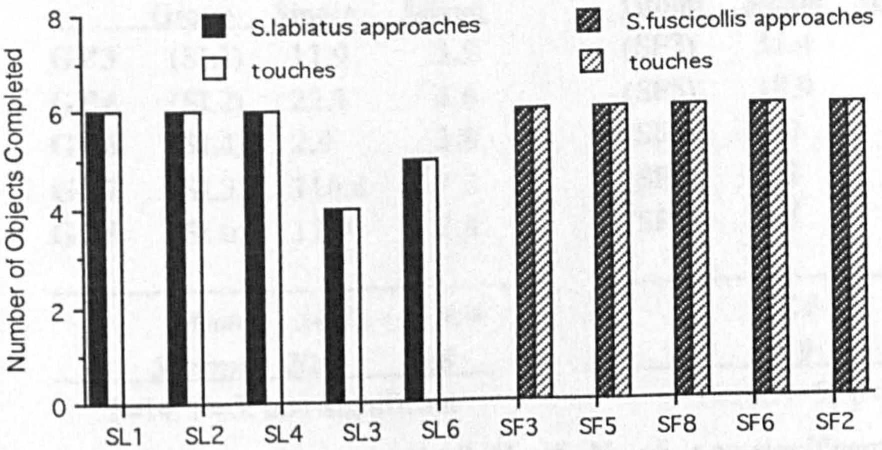


Figure 5.H : Total number of successful approaches and touches during Mixed-species trials.

This shows that in mixed groups, the *S. labiatus* reacted to significantly more floor area objects, when compared to single species trials, while *S. fuscicollis* reacted to a similar number of objects in both conditions.

5.9.3 Difference between approaches and touches : single vs. mixed groups.

The mean difference between approaching and touching (T-A) for both species, decreased dramatically when subjects were in mixed groups (Table 5.Q). This was only significant for *S. fuscicollis* (T=15, N=5, $p<0.05$), even though *S. labiatus* had a much more dramatic decrease. This was due to the extremely small T-A difference for SL4 during single species trials, which was less than that during mixed trials. All other groups had a reduced T-A difference. On the other hand, the frequency distribution of T-A differences, demonstrates a change in pattern for *S. labiatus*. This measure showed a difference between the species, where *S. labiatus* had a very different pattern of T-A differences while part of mixed groups (Figure 5.I). For *S. labiatus*, the modal T-A difference was greatly reduced when they were in mixed groups, reducing from 21-30 seconds in single species, to 0-1 seconds in mixed groups. Specifically, there was a relative increase in the amount of small T-A differences (0-1 & 2-3 second categories), found in *S. labiatus* during mixed presentations. These measures comprised only 31.3% (20/64) of single species trials, but 69% (60/87) of mixed-species trials.

Table 5. Q : Mean difference between approaching and touching novel objects in both single and mixed-Species groups.

	S. labiatus			*S. fuscicollis*		
	Group	Single	Mixed	Group	Single	Mixed
GP3	(SL1)	11.9	3.5	(SF3)	31.4	1.0
GP4	(SL2)	22.1	4.6	(SF5)	18.9	1.11
GP6	(SL4)	2.9	3.8	(SF8)	2.0	0.9
GP7	(SL3)	116.4	7.3	(SF6)	5.2	1.2
GP8	(SL6)	17.9	2.8	(SF2)	1.5	0.9
	Mean	*34.3*	*4.4*		*77.8*	*10.1*
	St.error	*20.7*	*0.8*		*5.9*	*0.1*
	T=14, N=5, non-significant			T=15,N=5, $p<0.05$		

Single Groups, U =8, $N_a=5$, $N_b=5$, non-significant

Mixed Groups, U =0, $N_a=5$, $N_b=5$, $p<0.01$

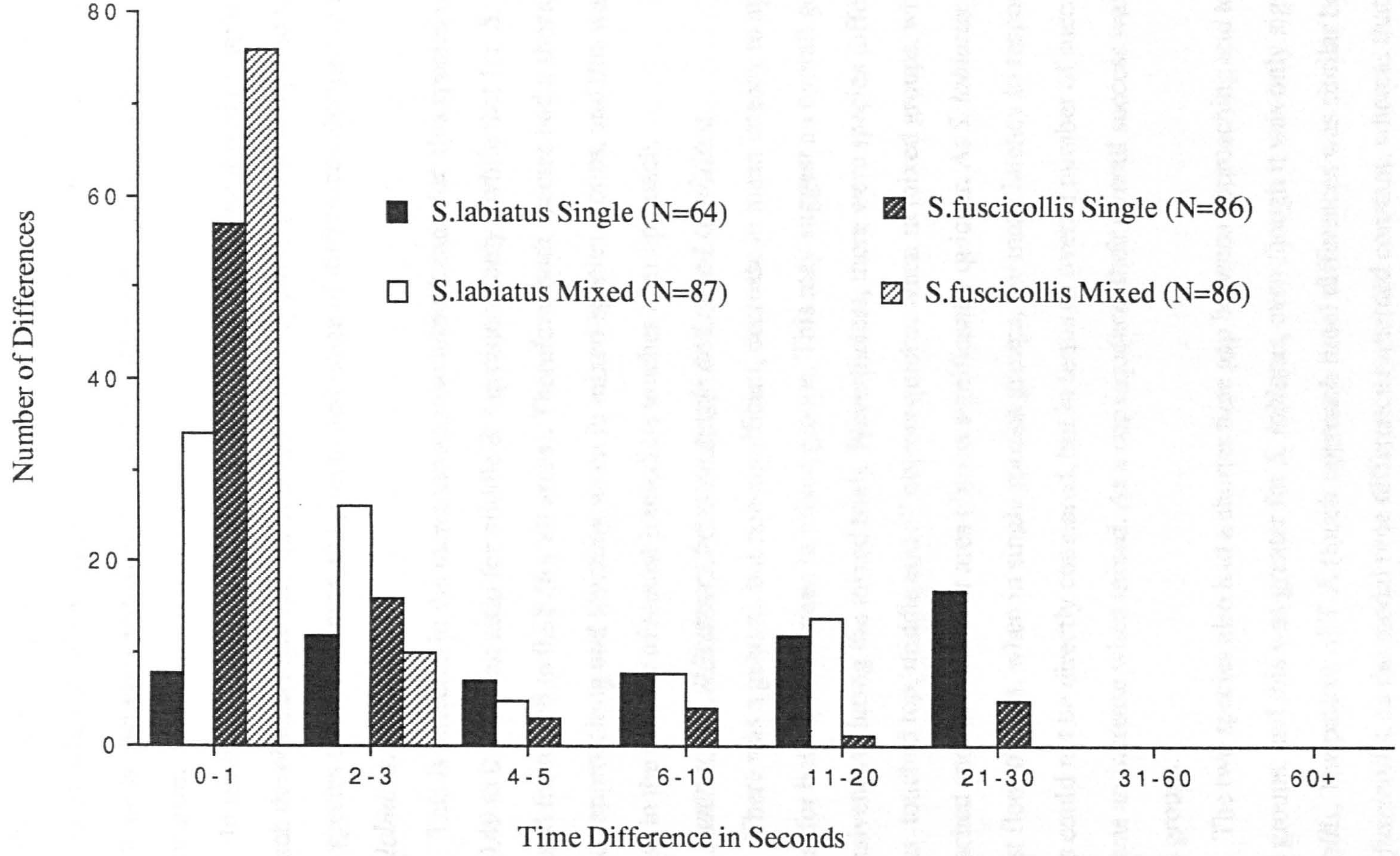


Figure 5.I : Approaching and touching differences in single and mixed-species tamarin groups.

In *S. fuscicollis* the overall pattern of T-A differences was similar in both conditions, although the amount of T-A differences under 30 seconds rose from 85% (73/86) in single groups up until 100% (86/86) in mixed groups. Overall, both species had a decreased delay between approaches and touches, when in mixed groups. However, the main finding was that *S. labiatus* were less likely to pause between approaching and touching during mixed-species trials, compared to when on their own.

In summary, there was a change by both species during mixed group trials; they tended to approach the objects relatively quicker after initial approach, when compared to response in single species trials. However, the pattern and range of differences changed more dramatically for *S. labiatus*.

This is reflected in the increased approach/touch ratio for this species which increased from 0.49 to 0.9 (mean ratio for middle & top objects only), while that for *S. fuscicollis* increased from 0.88 to 0.98 (for all areas). Therefore, both species had a shorter difference between approaching and touching when in mixed-species groups, and this was due to an increase in the number of almost immediate touches after approach.

5.9.4 Summary of differences between single and mixed conditions

There was a general, but non-significant, decrease in mean latency to approach novel objects, for both species when in mixed groups. This may suggest an overall general increase in responsiveness, during the mixed trials. Nevertheless, there were species differences, as *S. labiatus* touched top, middle and all objects quicker when in mixed groups, while *S. fuscicollis* approached and touched floor area objects significantly quicker. As *S. labiatus* failed to respond to most floor objects, when in single species groups, the mean latency to respond in mixed groups could not be directly compared, but in terms of overall number of successful responses, there was an increase when mixed. As a consequence, their overall success was also greater in mixed groups.

The two species also had a shorter time gap between approaching and touching when in mixed groups, and this was greater for *S. labiatus*, even though it was only significant for *S. fuscicollis*. The pattern of T-A (touch-approach time) differences was similar between conditions for *S. fuscicollis*, as the modal time difference remained constant, whereas that of *S. labiatus* moved down in value. This suggests that only *S. labiatus* had a reduction in hesitancy between approaching and touching, while in mixed groups. This is supported by *S. labiatus* having a significantly shorter latency to touch objects. Combining this with the above decrease in modal value of T-A difference, it appears that for *S. labiatus*, one main change over the two conditions, was the decrease in relative time to approach novel objects. This could not be explained by a general increase in overall responsiveness, as *S. fuscicollis* had no such change.

5.10 Discussion of Experiment 5.1.

In the current study, it was clear that the two species of tamarins differed in the manner which they responded to novel objects. In monospecific trials, the *S. labiatus* approached and touched novel objects presented at the top area, quicker than the *S. fuscicollis* did, and they also behaved similarly in mixed-species trials. This reaction can be predicted from the behaviour of these species in their wild state, where there is a divergence in the mean height used in the forest. In their natural habitat, *S. labiatus* are found at a higher mean height than the *S. fuscicollis*, and they also tend to be the first to enter feeding trees found in the upper canopy (see Chapter 2; Buchanan-Smith, 1989). This pattern is strikingly similar to the pattern of response to novel objects in the present study, and may reflect an increased amount of confidence on the part of *S. labiatus* when in this area, an increased familiarity with this area due to regular use, or a series of adaptations that has better prepared them for life in the upper reaches of the forest. It can be argued that the *S. labiatus* are adapted to life in the upper to middle areas of the forest, as they locomote through this area by quadrupedal locomotion, and leaping (e.g. Yoneda,1981,1984b), and conduct more vigilance up towards the sky (presumably for aerial predation threats) than their congeners (see Chapter 6). Similar behaviours have been noted for the other members of the *S. mystax* group (e.g. Heymann, 1990c; Peres, 1991,1993d; Terborgh, 1983). On the other hand, monospecific groups of *S. fuscicollis* were found to respond to more objects placed on the floor than the *S. labiatus*, and they were also first to approach and touch most floor area objects in mixed-species groups. This difference was most dramatic in monospecific groups, where the *S. labiatus* failed to approach and touch almost all objects placed on the floor, while *S. fuscicollis* responded to the majority of objects. Again this may be related to differences in their ecology, where *S. fuscicollis* spend more of their time in the lower reaches of the forest than their congeners (e.g. Yoneda, 1981). In mixed-species groups of *S. mystax* and *S. fuscicollis*, the *S. fuscicollis* have been shown to be the first to respond to feeding trees found in the lower areas of the forest (Peres, 1991), and to be first to approach traps placed low in the forest (Box & Morris, 1979). A similar response to traps and and artificially baited feeding platforms, has been shown in mixed-species groups of *S. labiatus* and *S. fuscicollis*, where the latter were first to respond to the presentation of the apparatus in their environment (Buchanan-Smith, 1989; Garcia, pers. comm.). This suggests that the *S. fuscicollis* react to stimuli placed in the lower area of their environment, before their congeners. Again this was found in the current study, and may be due to adaptations in the *S. fuscicollis* for life in the lower forest. These factors include, being more responsive than their congeners to potential terrestrial predation threats (Peres, 1991, for *S. mystax- S. fuscicollis* associations), having fore-limbs adapted for clinging to the large vertically orientated substrates found in the lower forest (Garber,1991), and having an insect foraging strategy that concentrates on extractive foraging in tree trunks, and the capture of large sized insects from in and around the forest floor (e.g. Garber, 1992,1993a,b; Terborgh, 1983; Yoneda,1981). Arguably, all these life-style patterns may account for the observed differences between the two species. This is complemented by the finding that the two species did not differ significantly in the mean latency to respond to objects placed in the middle of their enclosures, despite these strong differences in the top and floor area. This condition was the simplest, as the enclosures had a network of branches placed mainly around the middle of them, making the objects easily accessible, and both species spent much of their time in this area (pers. obs). However, this fails to explain the differences found in the other areas, and in the divergent way which each species responded to objects.

Specifically, the two species differed in their relative touch - approach time, where the *S. fuscicollis* had a more direct touch of the objects after the initial approach. This was found in both the single and mixed-species groups, although the gap in the mixed-species groups was lessened for both species. This may have been due to a general facilitation of responsiveness, due to repeated presentations of objects (e.g. Millar *et al.*, 1988), but may have been due to increased competitive pressures from the increased group size, or simply the presence of the other species. The quicker latency to touch objects after initial approach by *S. fuscicollis*, may again be related to life-style factors. In insect foraging, the two species show a dramatic divergence in preferred mode of capturing insects, where the *S. fuscicollis* use an extractive, manipulative foraging method, probing in to knotholes and crevices to gain items of embedded prey (see Garber, 1987, 1993b for reviews of insect foraging). They also quickly descend to the ground to immediately grab large insects, that are displaced from above, and from the foraging of their congeners (Peres,1991, 1992a). These data suggest that *S. fuscicollis* rely on manipulation to gain items of prey. This is not the same for *S. labiatus*, which rely on a very different way of gaining insect prey, and tend to capture a different set of prey items (Yoneda, 1981,1984b). A similar foraging method is used by all three members of the *S. mystax* group, who use a visually orientated search method, a "stalk and pounce" strategy, and generally gain smaller items of highly mobile prey predominantly from branches and leaves in the middle area of the forest (e.g. Buchanan-Smith, 1990a; Garber, 1993b; Peres, 1992a). This suggests a more visually orientated approach towards insects, and this reliance on vision prior to physical action (i.e. scan for potential prey before capturing them) may also apply to approaches towards objects. As the two species have been shown to diverge in the approach they utilise to forage for insects, it may be reflected in their responses to novel objects ; the manually orientated *S. fuscicollis* may contact an object relatively quicker than the *S. labiatus* when appears to use vision to a greater degree. Such a dichotomy has been found in other primate species, where Jolly (1964) found that variations in responsiveness to novelty in different species of prosimians' varied according to the way they approached food, while Fragaszy (1979) has also suggested that responses in *Callicebus moloch* and *Saimiri sciureus* can be related to feeding activity. In addition, it has been postulated that the high level of tactile responsiveness shown to objects by *Cebus apella*, can be related to their extensive range of manipulative skills, and to their use of a varied habitat in the wild (Visalberghi, 1988). These findings support the possibility that the use of manipulation during foraging by *S. fuscicollis* may influence their tendency to approach objects, while the visually orientated foraging of *S. labiatus* may contribute to relatively more visual inspection before tactile contact, thus resulting in a relatively slower approach. Overall, there is a tendency for *S. fuscicollis* to have a slightly quicker mean latency to approach and touch objects during completed trials, but as these differences failed to reach significance, this remains to be established. However, these notions remain to be tested empirically, through a controlled series of presentations of novel objects, given to both monospecific and mixed-species groups of tamarins.

Mixed-species groups are thought to give advantages to the individuals involved, through the interchange of behavioural responses, where this "behavioural facilitation hypothesis" suggests that the responses of one species can facilitate the reactions of the other species forming a mixed-species group (see Chapter 1). These responses can relate to at least two distinct variables; those related to the presence of food (e.g. Garber, 1988a,b), and to the presence of danger from predators (e.g. Peres, 1993d). The response or action that is facilitated between the species may be passed directly, where the actions of one individual or group can be used immediately by other individuals, for example the approach of *S. labiatus* to a feeding tree that has ripe fruit, may guide the *S. fuscicollis* to the resource. This type of facilitation was shown in Experiment 5.1, as when *S. labiatus* were part of mixed-species groups, they approached objects placed on the floor, only after they had been approached by *S. fuscicollis.* In the monospecific trials, they had failed to react to a similar set of objects placed on the floor, and this failure was found to be related to the position of the objects in their environment, not the objects themselves. This suggests that one of the possible advantages that *S. labiatus* accrue from being part of a mixed-species group, may be that they benefit from the responsiveness of *S. fuscicollis,* in the lower part of their environment. As *S. labiatus* allow their congeners to investigate this area before they respond, and bearing in mind that the *S. labiatus* are dominant and can forcefully take possession of resources (e.g. Buchanan-Smith, 1989; Pook & Pook, 1982, Chapter 2), means that they can benefit from the response of their congeners if the novel object is beneficial. Conversely, they have allowed the other species to investigate the object, and to take all the immediate dangers that the object may contain. There was no evidence of the the opposite pattern being found in the upper areas of the enclosure, but overall there was a decreased mean latency to approach objects for both species when part of mixed groups. This may reflect an increased confidence on the part of the participants when in mixed-species groups, but equally may reflect an increased amount of competition between the species. Again this remains to be tested. However, in the most detailed study of tamarin mixed-species groups, Peres (1991, 1993a) found that in *S. mystax* and *S. fuscicollis* groups, the more dominant *S. mystax* were first to enter and feed in large feeding trees, located in the upper and middle canopy areas of the forest, and they generally entered the tree, ate and then began to depart, before their congeners would enter the tree. The *S. fuscicollis* were first to enter small feeding trees in the lower areas of the forest, which they probably discovered opportunistically, but were subsequently displaced from such resources by their larger-bodied congeners. A similar pattern of restrictions in access to large feeding trees has been found in *S. labiatus* and *S. fuscicollis* mixed groups (Buchanan-Smith, 1989; Chapter 2). The small feeding tree situation probably parallells the floor objects in this study, while it was clear that in mixed-species groups during presentation of the top area objects, the *S. fuscicollis* tended not to approach these objects until the *S. labiatus* had departed (pers. obs.). However, due to the nature of the resources found in the different areas of their natural habitat (i.e. the large sized superabundant fruit sources are almost always found in large-crowned canopy trees : Peres, 1991), then the *S. fuscicollis* may benefit from the reactions of their congeners, even if they have to wait before they can reap these benefits.

Finally, it is worth noting that the enclosures used in the present study may have influenced its results, in a way which affected the species differently. This is because the two extremes of the cages, the top and floor, are only separated by a distance of approximately 2 metres. However, the findings from the floor area can be thought of as more robust than those from the top area, as the floor is always the lowest point of any situation, whether it is the forest floor or the floor of an enclosure. The top area may encompass a variety of different heights, in different situations. For example, the top area of the forest may be at a height of 30 metres or more, can this really be compared to a height of 2 metres in a captive enclosure ?. This is where the findings on ecological validity (Chapter 4) are important, as they suggest that, although the absolute height in captivity may be far lower than that in the wild situation, the relative partitioning of the available environment is very similar in both conditions. Therefore, it is likely that the findings of the present study may be generalised to the situation in the wild.

5.11 Summary of Experiment 5.1.

Both species behaved as predicted, as *S. labiatus* approached and touched top area objects significantly quicker, and *S. fuscicollis* approached and touched floor areas objects quicker in both conditions, and in mixed groups reacted to them before *S. labiatus* did. They also reacted to more quickly to objects overall. These differences in response may be related to life-style patterns under natural conditions, where the *S. labiatus* are usually found at a higher mean height than their congeners, which are generally found nearer to the ground. Differences in mean touch -approach time (T-A) occurred where *S. fuscicollis* were found to have a shorter T-

A time, and this may be related to the tendency for *S. fuscicollis* to manipulate objects, while *S. labiatus* used a visually orientated foraging technique. There was also an overall decrease in reaction times for both species, comparing single and mixed trials, and it suggests that the reaction of one species may effect the congener.

The *S. labiatus* are shown to exhibit a pattern of responses which mirror the behaviour of tamarins in mixed-species groups in the wild. They seem to benefit from the reactions of the *S. fuscicollis* in the lower area of the enclosures, and *S. labiatus* will contact these objects when in mixed groups, only after they have been approached by the *S.. fuscicollis.* The *S. fuscicollis* may benefit from the improved reactions of the *S. labiatus* in the top areas, although they may be forced to wait for benefits due to the dominance of their congeners.

5.12 Section 5.2 : Response of tamarin groups to the presentation of objects which may or may not be paired with food.

5.12.1 General introduction.

It has been clearly shown that both species of tamarins will readily react to the presentation of objects within their environment (Experiment 5.1). This produced a useful dichotomy between the species, where their reactions were suggestive of differences in their life-styles. However, this experiment only demonstrated that the species could react differently to novel objects placed in different areas of their cage, providing little evidence of how they might use this information. This may have been because the objects had little or no direct use for the animals.

The present experiment set out to remedy this potential problem, by testing the reaction of both species to the repeated presentation of novel objects that were either associated with food or not associated with food. This gave the species the opportunity to react to a situation that was equivalent to the discovery of a new food resource. The experiment was based on the work of Menzel & Juno (1982), who showed that *S. fuscicollis* could differentiate between food and non-food objects, after a single trial.

5.12.2 Learning and food for tamarins.

In the wild, tamarins spend much of their time trying to find and process items of food (Chapter 1), and they live in a complex three-dimensional environment, where they need to remember the location and nature of resources, and to navigate back to them when required (e.g. Garber, 1989,1993b; Garber & Hannon,1993; Garber *et al.*, 1993). They need to have sufficient ability to detect and use opportunistically new food resources when they discover them (e.g. Peres,1991; Terborgh, 1983). They also have to make decisions regarding the use of resources, whether to defend them, how long to remain there, where to move off to, how to deal with unfamiliar situations etc. (e.g. Dolins & Garber, 1994; Garber, 1989). This suggests that they require a detailed knowledge of their environment.

In captivity, tamarins have been shown to be able to recognise, and learn to respond to, a variety of novel objects (e.g. Menzel & Menzel, 1979; Menzel & Juno, 1982) and novel social stimuli (e.g. French & Inglett, 1991). Tamarins have demonstrated an ability to "learn and remember the visual appearances and the locations and orientations...of objects" (Menzel & Juno, 1985: 147). This suggests that captive groups of tamarins are able to learn properties related to objects, and are able to respond differentially to a variety of different objects. For tamarins, much of their time is spent in the acquisition and consumption of items of food (Garber, 1993b; Peres, 1991; Terborgh, 1983), and foraging is an essential part of their behavioural repertoire. It is no major surprise, therefore, that captive groups of *S. fuscicollis* (Menzel & Menzel,1979) and *S. oedipus* (Dolins, 1993), have been found to quickly learn to respond to objects associated with the presence of food, even under demanding conditions. For example, Dolins (1993) has suggested that captive *S. oedipus* are able to use the spatial relationships between 2 abstract cues to discover hidden food items, while Menzel & Juno (1985) were able to demonstrate that *S. fuscicollis* could detect a novel object out of a set of at least 30 objects, and could retain information concerning the location of objects that had previously contained food. These studies show that at least 2 species of tamarins can learn about the presence of food, when it was linked to various objects.

The reaction of tamarins to the presentation of novel objects which may or may not be food items is examined in this section. Following the work of Menzel & Juno (1982), it was hypothesised that subjects of both species could learn about the availability of food which is paired with certain classes of objects. This was to be tested in monospecific groups of both species. It was also decided to create a situation of divergent behaviour, where the class of object tested would have conflicting status for both species (i.e. food for one species = non-food for the other). In effect, this created a situation were each species would have a different pattern of behavioural response which could be transferred between the species. This would produce a test of the "behavioural facilitation hypothesis", as each species would have responses related to the presence of food, and their congeners could learn to respond to these object as food through the facilitation of the reactions of their congeners. However, no specific claims are made, other than that the food associated response learned by one species will allow the other species to quickly learn to react to the "food object" more than to non-food objects.

In single species groups, the following predictions are tested :

1) Both species should learn to respond differently between presentations of objects which have been previously paired with food, and those which have not. The objects paired with food, will be approached and touched in a faster latency.

2) If both species learn to respond to objects paired with food, then if the same objects have divergent status (i.e. paired with food for *S.labiatus*, not paired with food for *S.fuscicollis* & not paired with food for *S.labiatus*, paired with food for *S.fuscicollis*), then both species should learn to respond differently to the <u>same</u> objects.

5.13 Methods.

<u>Experiment 5.2A The presentation of food and non-food objects.</u>

Do the 2 species of tamarins both learn to react differently to a series of food and non-food objects ?

<u>5.13.1 Subjects.</u>

The groups tested in this study were 6 groups of *S. labiatus* (SL1, SL2, SL3, SL4, SL5, SL6) and 6 groups of *S. fuscicollis* (SF1, SF2, SF3, SF5, SF6, SF8), each housed in individual indoor / outdoor cages at Belfast Zoological Gardens. Exact details of groups are presented earlier (see Chapter 3).

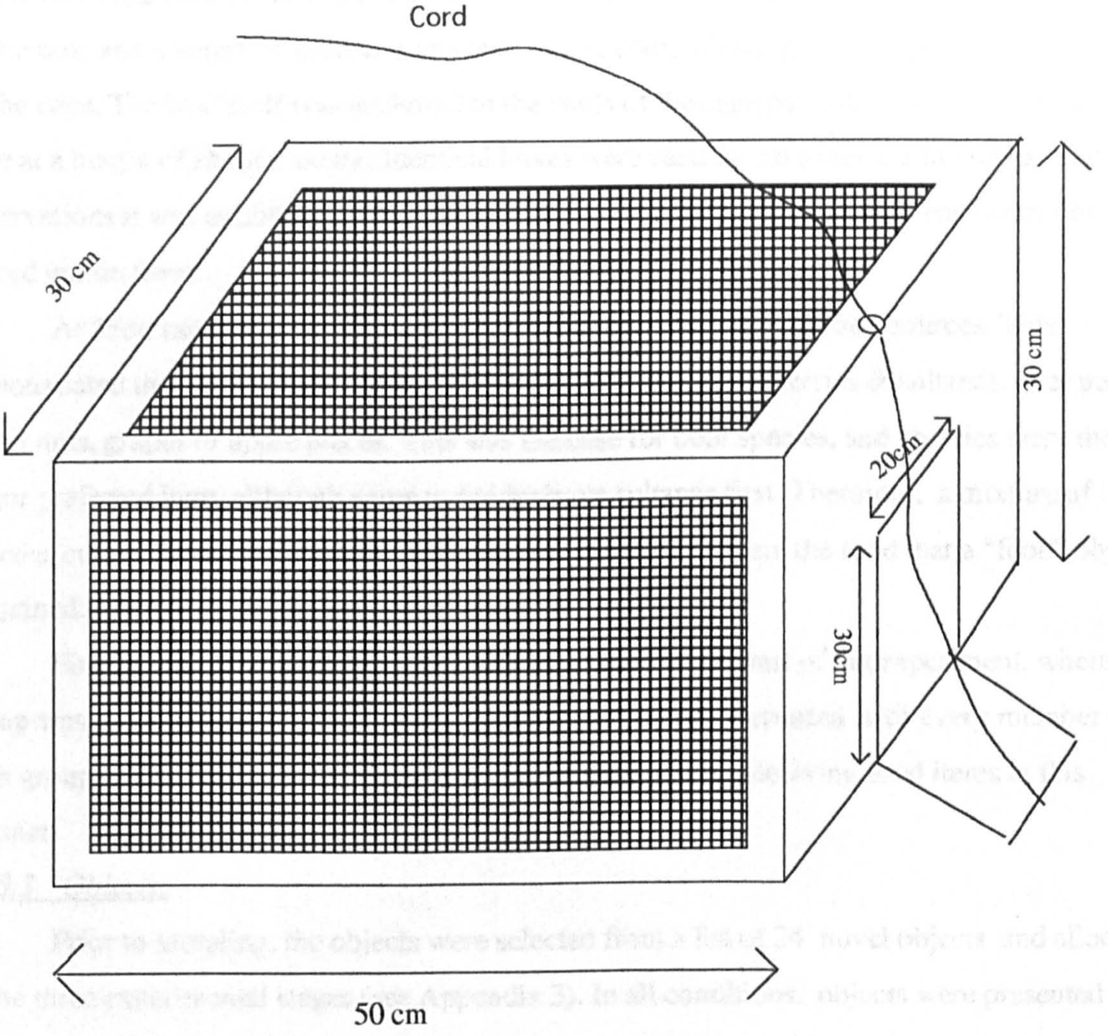


Figure 5.J : Plan of the box used during food and non-food object presentations.

5.13.2 Pilot study.

An experimental box was made, based on that used by Menzel & Menzel (1979) and Menzel & Juno (1982). The box was constructed using a 0.5 cm thick plywood back, front and floor (Figure 5.J). The top and sides were constructed from 0.5cm metal weldmesh, and the whole box measured 50cm x 30cm x 30cm. A 15cm x 20cm hinged door was located at the front of the box, and a length of cord was attached to this door, allowing it it be opened from outside of the cage. The box itself was anchored to the walls of the cage by nails and tied securely with wire at a height of about 1 metre. Identical boxes were used for all groups, and during pilot observations it was established that both species would readily approach and encounter objects placed within them.

As food items were to be used, there was a test for potential food sources. This demonstrated that the animals had a strong preference for glacé cherries & sultanas, over peanuts, brazil nuts, grapes or apple pieces. This was the case for both species, and cherries were the major preferred item, although some individuals ate sultanas first. Therefore, a mixture of two cherries cut up into approximately 10 pieces, and 20 sultanas were the food that a "food" object contained.

Finally, a training protocol was performed prior to the start of the experiment, where each group was fed for at least 5 days, inside their boxes. This was repeated until every member of each group would readily enter the box, and was familiar with receiving food items in this manner.

5.13.3 Objects.

Prior to sampling, the objects were selected from a list of 24 novel objects and allocated to the three experimental stages (see Appendix 3). In all conditions, objects were presented for 10 minute sample sessions.

5.13.4 General methods and procedure.

Once it was established that each group would enter their respective boxes, the experiment was started. Observations were carried out between July & September 1993, and between May & July 1994. All objects were hollow, in order that food could be hidden inside, so that the object had to be manipulated, if the subjects were to find the food. The objects themselves were placed into the middle of the testing box.

Experimental set-up.

The experiment was conducted in three distinct stages :

Stage I : Three non-food (NF) objects, each receiving 2 individual trials, were conducted to see if the reaction reduced on second presentation (Lose-Shift). The same objects were used for both species.

Stage II : Six objects (3 x food [F] & 3 x non-food [NF]), are each presented on four consecutive days, given as 3 learning trials (with food for F objects, none for NF objects) followed by one test trial (no food for either condition). Again objects used were identical for both species.

Stage III : A further set of 6 (3 x NF & 3 x F) objects , each getting 3 learning and 1 test trials, but their object class was contradictory for each species (i.e. a Food object for *S. labiatus* was a non-food object for *S. fuscicollis* [F(Sl) / NF(Sf)], and a Food object for *S. fuscicollis,* was a non-food object for *S. labiatus* [NF(Sl) / F(Sf)]).

In the first two Stages, both species have exactly the same learning about non-food items (Stage I & II Non-food), and food items (Stage II Food). In the third stage, the basic pattern was that each species received a set of 3 objects which were paired with food for that species only, as the same objects were presented as non-food objects to the other species. Therefore, both species have divergent experiences of the properties of the same objects, which relate to the presence or absence of food items. This stage was conducted in order to set up a test of the "behavioural facilitation hypothesis" in mixed-species groups, as monospecific groups of both species each had a different set of behavioural responses relating to the presence of food, which could be facilitated interspecifically.

Presentation of objects.

Stage I objects were each presented for 2 consecutive days. Stage II & III objects were presented as 4 distinct trials over four consecutive days, the first three containing food (if they were food objects), the fourth was a test session containing no food. This was so that test trials would not have the presence of food as a confounding factor, and the time spent on the box would be due entirely to a learned "expectation" of food. The order of presentation (i.e. object class) was randomly varied and time of day was counterbalanced, to avoid possible order effects. Each group received only one sample session per day. During all trials, groups of other tamarins adjacent to the group being studied were locked into their respective indoor areas, while the study group was locked out.

The session was conducted as follows ; the chosen object was placed inside the box, and the door shut. The study group were locked into their outdoor area, and the session began approximately 30 seconds later, when the door was opened to allow access to the object, and carried on for a period of 10 minutes.

Instantaneous scan samples were recorded an a checksheet (Appendix 1), at 15 second intervals. The main measure was simply the number of animals in or on the box (i.e. 0,1, or 2) at each sample interval. This was measured as the number of box visits (BV), where it was defined as one monkey in, or on, the box at a sample interval. Other measures included ; the latency from opening of the box, until the initial approach into the box, where the first animal moved to within <15cm of the object, and the latency until the first touch of the object were noted. In food trials, the latency from opening until the first individual found a food item, was also recorded. In all cases, individual trials were 10 minutes long, giving 40 sample points per session.

Baseline.

In order to evaluate the amount of time the animals would use the box, in absence of any stimuli inside, it was necessary to conduct baseline trials. Each group received a set of four x ten minute trials, where the number of animals in, or on, the box at each sample interval were recorded. This was conducted before the presentation of experimental trials, and was used a control situation, with which to compare trials containing objects

5.14 Results.

5.14.1 Baseline observations.

The two species had a very similar mean amount of visits per individual, to the box during baseline trials, where no objects were present (Table 5.R). In terms of mean number of visits to the box, *S. fuscicollis* had a slightly larger mean number of visits per session (3.8, St. error 0.44), but this was only slightly greater than that shown by *S. labiatus* (3.4, St. error 0.25), and was consequently a non-significant difference (U=14.5, N_a=6, N_b=6, non-significant).

Table 5.R : Number of box visits (BV's) during baseline observations, where a visit was defined as one monkey in or on the box at any sample point. (Total visits possible = total number of sample points X number of monkeys in a group).

Group	N	Total visits (in 4 sessions)	Mean no. of visits per session	Mean no, of visits per ind. per session
SL1	2	20	5	2.5 (0.35)
SL2	2	24	6	3.0 (0.84)
SL3	2	31	7.8	3.9 (0.85)
SL4	2	32	8	4.0 (0.2)
SL5	5	55	13.75	2.8 (0.25)
SL6	2	32	8	4.0 (0.36)
Species mean				**3.4 (0.25)**
SF1	4	84	21	5.3 (1.7)
SF2	2	35	8.75	4.4 (0.55)
SF3	2	24	6	3.0 (1.0)
SF5	2	36	9	4.5 (0.29)
SF6	2	22	5.5	2.8 (0.43)
SF8	2	22	5.5	2.8 (1.1)
Species mean				**3.8 (0.44)***

*Mann Whitney Test Between Species : U = 14.5, N_a=6, N_b=6, non-significant.

5.14.2 *Stage I - "lose-shift"*

Table 5.S shows that both species followed the classic "lose-shift" pattern, whereby they responded less to the second presentation of an object that did not give them any benefit (i.e. did not contain any food). Specifically, there was a significantly reduced mean number of visits to the box (BV's) on second presentation for both species (T=21, N=6, $p<0.05$). This suggests that both species may be able to learn about the properties of an object after a single presentation, and would respond according to that information. The results were compared to the baseline results, and it was clear that the initial presentation had a significantly greater number of BV's than baseline (T=21, N=6, $p<0.05$), but by the second presentation, the results did not significantly deviate from those of the baseline presentation. Comparing the two species, the *S. fuscicollis* had significantly more first presentation BV's than *S. labiatus* (U=6, N_a=6, N_b=6, $p<0.05$), and although this pattern also occurred in the second presentation, it was not significant (U=13,N_a=6, N_b=6, non-significant).

Table 5.S : Mean number of box visits during lose / shift observations. Scores are mean number of box visits per individual, and bracketed values are standard errors.

Group	N	Baseline	First Presentation	Second Presentation
SL1	2	2.5 (0.35)	6.3 (0.6)	2.2 (0.6)
SL2	2	3.0 (0.84)	4.3 (0.93)	3.5 (0.76)
SL3	2	3.9 (0.85)	4.8 (0.83)	1.8 (0.44)
SL4	2	4.0 (0.2)	6.3 (0.17)	3.3 (0.17)
SL5	5	2.8 (0.25)	6.7 (1.1)	3.9 (0.44)
SL6	2	4.0 (0.36)	8.2 (0.17)	4.8 (0.17)
Mean		**3.4 (0.25)**	**6.1 (0.57)**[1]	**3.3 (0.45)**[2]
SF1	4	5.3 (1.7)	11.2 (1.7)	7.7 (0.83)
SF2	2	4.4 (0.55)	9.0 (2.1)	3.2 (0.7)
SF3	2	3.0 (1.0)	8.3 (1.2)	4.2 (0.44)
SF5	2	4.5 (0.29)	6.8 (2.2)	2.8 (1.1)
SF6	2	2.8 (0.43)	7.0 (0.8)	6.7 (2.5)
SF8	2	2.8 (1.1)	6.2 (0.3)	3.0 (0.6)
Mean		**3.8 (0.44)**	**8.0 (0.75)**[1]	**4.6 (0.86)**[2]

[1] Mann-Whitney: *S. labiatus* Vs. *S. fuscicollis*, First presentation
$U=6$, $N_a=6$, $N_b=6$, $P < 0.05$

[2] Mann-Whitney: *S. labiatus* Vs. *S. fuscicollis*, Second presentation
$U=13$, $N_a=6$, $N_b=6$, non-significant

An examination of the number of approaches and touches of objects, show that the first presentation received more overall attention than the second (Table 5.T). Both species approached and touched all first presentations, but only approached 66.7% (12/18) of second presentations. Indeed, both species were reluctant to touch objects during the second presentation, and *S. fuscicollis* touched only 50% (9/12) of objects, while *S. labiatus* touched only 27.8% (5/18). Although, *S. labiatus* had a quicker mean response to first presentation of objects, this was not significantly different for either approach ($U=14$, $N_a=6$, $N_b=6$, non-significant) or touch ($U=12$, $N_a=6$, $N_b=6$, non-significant). As both species did not approach and touch many second presentation objects, it was not appropriate to compare these latencies statistically. However, both species had a similar mean approach time, and *S. labiatus* had a quicker mean touch time.

Table 5.T : Mean latency and overall success in approaching and touching objects during “lose-shift” presentations, for two species of tamarins.

First Presentation

S. labiatus	Mean Approach[1] =	20.7 sec (St.error 5.0)	[N=18]
	Mean Touch[2] =	43.8 sec (St.error 14)	[N=18]
S. fuscicollis	Mean Approach =	26.9 sec. (St.error 6.3)	[N=18]
	Mean Touch =	45.6 sec (St.error 7.0)	[N=18]

[1] Mann-Whitney, U = 14, N_a=6, N_b=6,non-significant.

[2] Mann-Whitney, U = 12, N_a=6, N_b=6,non-significant.

Second Presentation

S. labiatus	Mean Approach =	62.3 sec (St.error 5.0)	[N=12]
	Mean Touch =	55.4 sec (St.error 23.1)	[N=5]
S. fuscicollis	Mean Approach =	59.5 sec. (St.error 14.8)	[N=12]
	Mean Touch =	82.4 sec (St.error 19.8)	[N= 9]

5.14.3 Stages II + III - Reaction to the presentation of different categories of objects.

Both species were shown to respond differentially between test trials (i.e. presentations containing no food) of food [F], non-food [NF] and divergent status [F(Sl) / NF(Sf) & NF(Sl) / F(Sf)] objects (Figure 5.K). Although the results of both species were collected for all four trials, the analysis concerns only those results found during the final “test” trial on any object. The full data set is found in Appendix 4.

Differences shown during test trials can be compared in terms of ;

(a) differences within each category of object, and **(b)** differences between the various categories of objects. These are examined separately.

5.14.4 Differences within object categories.

The species are compared on three different measures, i) the mean number of box visits (BV’s) per category, ii) the mean latency to approach an object in each category, on completed trials, and iii) the mean latency to touch an object, in each category. These comparisons are carried out per object category.

Food Objects [F] (same for both species)

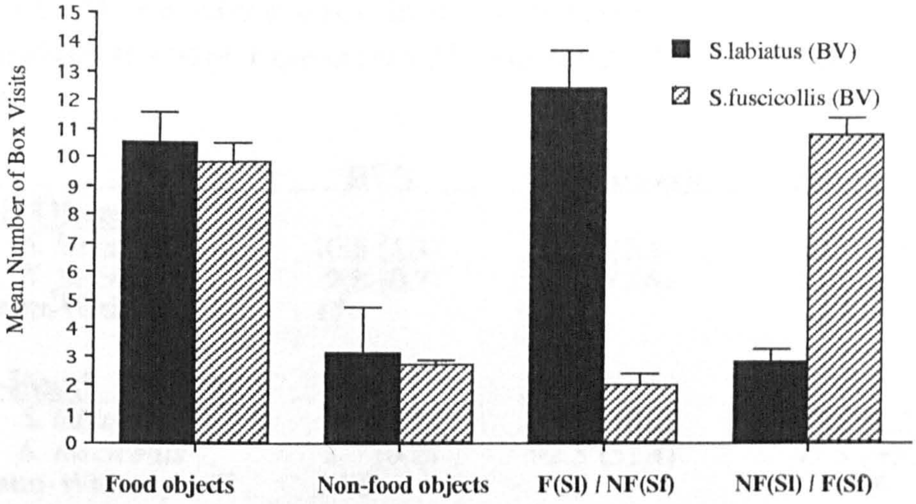
Figure 5.K shows that in test trials, *S. labiatus* had a larger mean number of BV's per individual, and these objects were approached and touched in a quicker mean latency. However these differences were not significant for either BV's ($U=17$, $N_a=6$, $N_b=6$, non-significant), latency to approach ($U=14$, $N_a=6$, $N_b=6$, non-significant), or latency to touch ($U=13$, $N_a=6$, $N_b=6$, non-significant). As test trials did not contain food items, the species were compared on mean latency to eat food on first trials. This showed that both *S. labiatus* (mean 47.7 sec. St.error 17.5) and *S. fuscicollis* (mean 59.8 sec. St.error 28.7) had a relatively similar mean time to detect food on first trials, and so the difference was not significant ($U=17$, $N_a=6$, $N_b=6$, non-significant). The two species reacted similarly to the presentation of objects containing food, and learned to respond to these objects, and not only to the food itself.

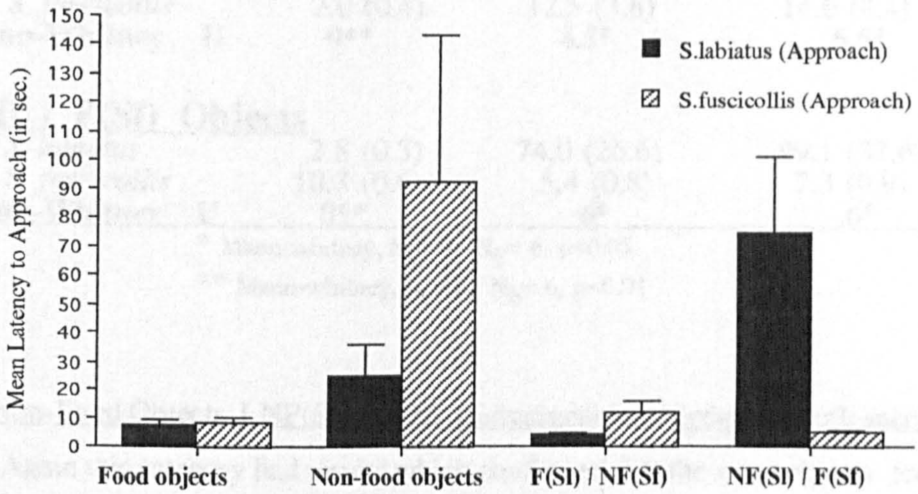
Non-Food Objects [NF] (same for both species)

Table 5.U shows that once again the *S. labiatus* had a slightly larger mean number of BV's, but this was not significantly greater ($U=14.5$, $N_a=6$, $N_b=6$, non-significant). This time the *S. labiatus* had a much mean quicker approach and touch time, but both were non significant (for approach $U=16$; for touch $U=11.5$, $N_a=6$, $N_b=6$, non-significant). Therefore both species had a similar response to NF objects (Figure 5.K).

Food /Non-Food Objects [F(Sl) / NF(Sf)] (divergent knowledge for both species)

In this category, as only the *S. labiatus* was presented with food, they had a significantly larger mean number of BV's, than *S. fuscicollis* ($U=0$, $N_a=6$, $N_b=6$, $p<0.01$). This was predicted, as was the significantly quicker mean latency to approach ($U=4$, $N_a=6$, $N_b=6$, $p<0.05$) and touch objects ($U=5.5$, $N_a=6$, $N_b=6$, $p<0.05$). This demonstrates that the two species responded to the same objects in a divergent manner, to *S. labiatus* they were "food" objects, whereas to *S. fuscicollis* they were non-food (Table 5.U, Figure 5.K).


I : Mean number of box visits


II : Mean latency to approach objects

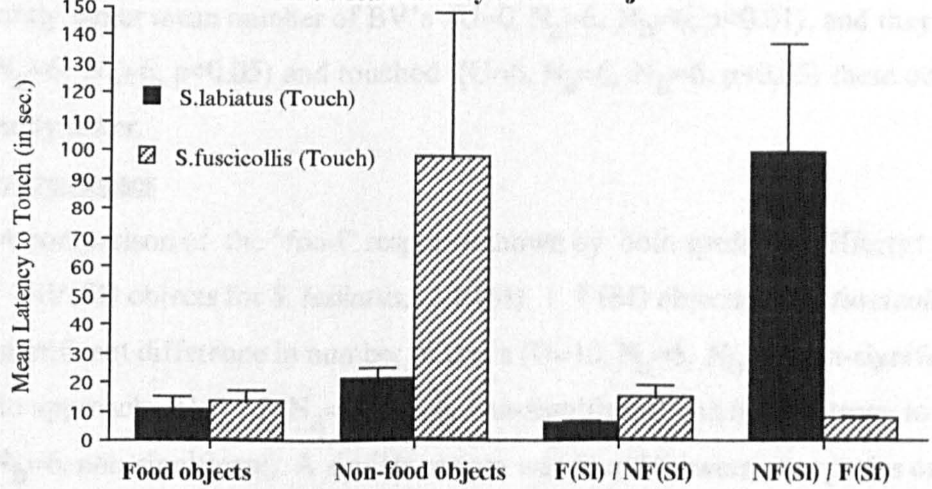

III : Mean latency to touch objects

Figure 5.K : Mean Number of BV's, latency to approach and touch, during test trials. Bars show standard errors.

Table 5.U : Mean number of box visits (BV's), and mean latency to approach and touch objects during phases II + III of Experiment 5.2A. Bracketed values are standard errors of the mean scores.

	BV's	Approach	Touch
Food Objects			
S. labiatus	10.5 (1.1)	6.6 (2.3)	10.5 (4.6)
S. fuscicollis	9.8 (0.7)	8.0 (2.6)	13.0 (4.0)
Mann-Whitney U	**17**	**14**	**13**
Non-Food Objects			
S. labiatus	3.1 (1.7)	25.2 (10.5)	20.6 (4.2)
S. fuscicollis	2.7 (0.2)	92.3 (51.4)	97.5 (50.2)
Mann-Whitney U	**14.5**	**16**	**11.5**
F(Sl) / NF(Sf) Objects			
S. labiatus	12.4 (1.3)	4.2 (0.7)	5.8 (0.7)
S. fuscicollis	2.0 (0.4)	12.5 (3.8)	14.6 (4.4)
Mann-Whitney U	**0****	**4.5***	**5.5***
NF(Sl) / F(Sf) Objects			
S. labiatus	2.8 (0.5)	74.0 (26.6)	99.1 (37.6)
S. fuscicollis	10.8 (0.6)	5.4 (0.8)	7.3 (0.9)
Mann-Whitney U	**0****	**6***	**6***

* Mann-whitney, N_a= 6, N_b= 6, p<0.05

** Mann-whitney, N_a= 6, N_b= 6, p<0.01

Food /Non-Food Objects [NF(Sl) / F(Sf)] (divergent knowledge for both species)

Again this category had results which confirmed that the same objects produced a different class of response in the each species (Table 5.U). This time the *S. fuscicollis* had a significantly larger mean number of BV's (U=0, N_a=6, N_b=6, p<0.01), and they approached (U=6, N_a=6, N_b=6, p<0.05) and touched (U=6, N_a=6, N_b=6, p<0.05) these objects significantly faster.

Divergent responses

A comparison of the "food" response shown by both species to different objects (i.e. **F(Sl) / NF(Sf)** objects for *S. labiatus*, **NF(Sl) / F(Sf)** objects for *S. fuscicollis*), failed to show a significant difference in number of BV's (U=10, N_a=6, N_b=6, non-significant), mean latency to approach (U=11.5, N_a=6, N_b=6, non-significant) and mean latency to touch (U=12, N_a=6, N_b=6, non-significant). A similar pattern was found between the species on "non-food" responses, (i.e. NF(Sl) / F(Sf) objects for *S. labiatus*, F(Sl) / NF(Sf) objects for *S. fuscicollis*), where they had a similar number of BV's (U=10.5, N_a=6, N_b=6, non-significant) and no significant differences between mean approaching and touching latencies (U=8, N_a=6, N_b=6, non-significant), even though *S. labiatus* had a much slower mean latency to approach and touch objects "non-food" objects than *S. fuscicollis* (Figure 5.K).

In summary, both species followed the predicted pattern of response, and the only significant differences in object categories were found where conflicting knowledge was given to each species independently. However, the response of each species to objects which were or were not paired with food was maintained, and similar amounts of BV's and mean latencies to respond, were shown to the same categories of objects. The two species were shown to produce divergent responses to the same objects, and these are further examined in Experiment 5.2C.

5.14.5 Differences between object categories.

A pairwise comparison between the four individual object categories, demonstrates differences between the mean BV's per individual, the mean approach time and the mean touch time, in different categories (Table 5.V).

Mean number of BV's

In *S. labiatus* the mean value of BV's was significantly larger for both object categories which had been paired with food (i.e. F, F(Sl) / NF(Sf)), when they were each compared to those which were not (i.e. NF, NF(Sl) / F(Sf)), and all comparisons had a similar level of significance (T=21, N=6, $p<0.05$). The two object categories which were paired with food, did not differ significantly from each other (T =13.5, N=6, non-significant), nor did the two object categories which were not paired (T =13.5, N=6, non-significant).

For *S. fuscicollis*, the two object categories paired with food (i.e. F, NF(Sl) / F(Sf)) were also significantly different from the two which were not (i.e. NF, F(Sl) / NF(Sf)), and all comparisons were equally significant. In addition, there were no significant differences between the two food paired (T =15, N=6, non-significant) and two non-food paired object categories (T =18, N=6, non-significant).

Mean latency to approach and touch objects.

The *S. labiatus* had a similar pattern of significant differences, between categories, in the mean latency to approach and touch objects, as they previously had to BV's (Table 5.V).

Comparing food and non-food categories, all differences were equally significant ($T=21$, $N=6$, $p<0.05$), except between F(Sl) / NF(Sf) and NF / F, which had one group omitted from the test due to a tie in scores ($T=15$, $N=5$, $p<0.05$). The latency to approach the two food categories were not significantly different ($T=8$, $N=5$, non-significant) nor did they have a significantly different mean latency until touched ($T=12$, $N=6$, non-significant). However, the mean time to approach and touch was significantly faster for objects in the NF(Sl) / F(Sf) categories, when compared to NF objects ($T=20$, $N=6$, $p<0.05$).

Table 5.V : Pairwise comparison of the mean number of box visits (BV's), and the mean latency to approach and touch the 4 categories of objects used in Experiment 5.2A. Values are presented as T values, for the Wilcoxon Signed Ranks Test.

	S. labiatus			***S. fuscicollis***		
	BV's per ind.	App.	Tou.	BV's per ind.	App.	Tou.
F vs. NF	**21***	**21***	**21***	**21***	**20***	**20***
F vs. F(Sl) / NF(Sf)	**15**	**8**	**12**	**21***	**15**	**11**
F vs. NF(Sl) / F(Sf)	**21***	**21***	**21***	**15**	**8**	**9**
NF vs. F(Sl) / NF(Sf)	**21***	**21***	**21***	**18**	**16**	**12**
NF vs. NF(Sl) / F(Sf)	**13.5**	**20***	**20***	**21***	**21***	**21***
F(Sl) / NF(Sf) vs. NF(Sl) / F(Sf)	**21***	**21***	**15****	**21***	**18**	**18**

* $N = 6$, $p<0.05$, ** $N = 5$, $p<0.05$

In *S. fuscicollis*, the mean latency to approach and touch food objects, was significantly quicker than that shown towards NF objects (both $T=20$, $N=5$, $p<0.05$). However, when comparing F(Sl) / NF(Sf) objects with food objects, these differences were not significant. Specifically, although food (F) objects were approached and touched quicker, these differences were not significant (for approach $T=15$; for touch $T=11$, $N=6$, non-significant), and a similar pattern was found for approaches and touches to NF(Sl) / F(Sf) objects ($T=18$, $N=6$, non-significant).

<u>Practice effects.</u>

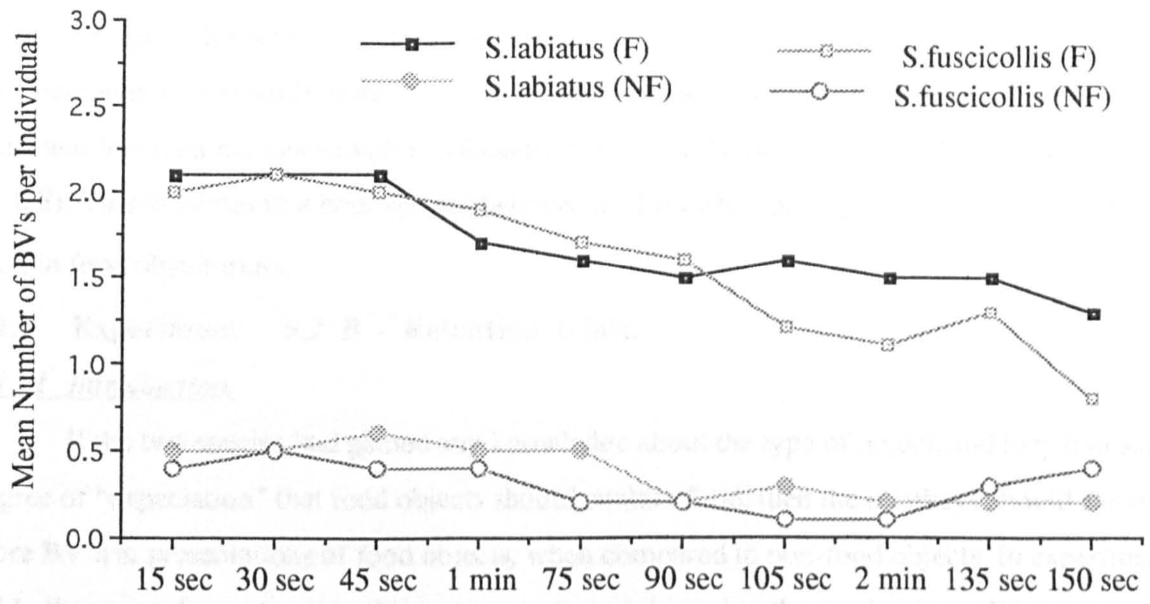
As phase II presentations were given before phase III, the remained the possibility of order or practice effects. The two food categories and the two non-food categories were examined. For both species, the phase III food-paired objects had slightly more BV's, and were approached in a slightly quicker mean time. These differences were all non-significant (see Table 5.V). In non-food presentations, there was a slight reduction in BV's for both species, but while *S. labiatus* had a significantly larger mean latency to both approach and touch phase III objects, *S. fuscicollis* had a reduction in mean latency. This suggests that the two species may differ in their reaction towards persisting to approach potential food sources, although both approached and touched a similar number of phase III non-food objects (*S. labiatus* ; approached 14, touched 12 : *S. fuscicollis* ; approached 13, touched 13). Therefore no clear pattern was found.

Summary.

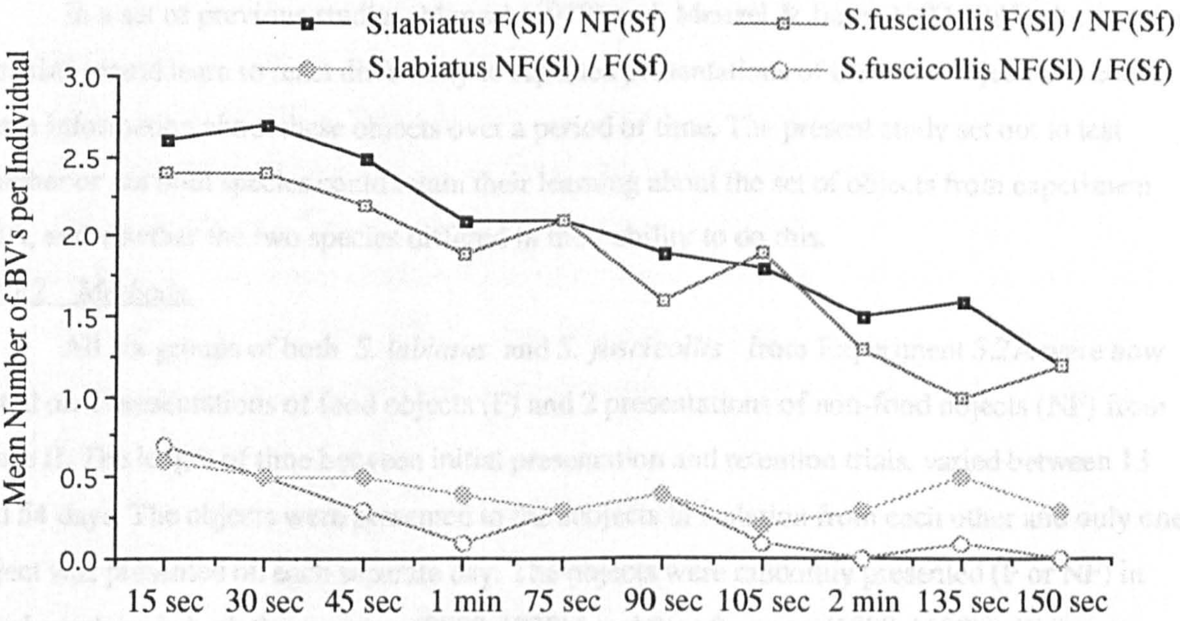
Overall, the two species reacted towards food objects in a different way from those objects that were not presented with food. The strongest effect was that the number of animals visiting the box (BV's) was significantly greater on object categories which had been paired with food. In *S. labiatus*, the latency to approach and touch also followed this pattern, where food-paired objects were approached and touched significantly quicker. In *S. fuscicollis*, the effect was not as strong, as not all approaches and touches were significantly quicker, but all mean approaches and touches were quicker in presentations of food-paired objects. There was a slight practice effect, where the phase III presentations had a more extreme effect, in that non-food objects had a reduced number of BV's, and food objects had an increased number of BV's which were approached and touched quicker.

5.14.6 Box visits during the first 2.5 min. of trials.

In order to examine the way both species initially responded to each object category, the mean number of box visits (BV's) per individual was compared during the first 10 sample intervals (2.5 minutes) and this was also compared between the species (Figure 5.L). The two food categories were found to have a significantly larger mean number of BV's than the both non-food categories, for both species and all pairings ($T=21$, $N=6$, $p<0.05$). The two species did not differ significantly between the amount of BV's they made to both, phase II food (F) objects ($U=14.5$, $N_a=6$, $N_b=6$, non-significant) and non-food (NF) objects ($U=12$, $N_a=6$, $N_b=6$, non-significant).



Phase II [Food & Non-Food objects]



Phase III [F(Sl) / NF(Sf) & NF(Sl) / F(Sf) objects]

Figure 5.L : Mean total number of box visits (BV's) per individual, summed over the first 2.5 minutes of all test trials per condition (3 objects per condition).

A similar pattern was found in both phase III food objects (U=8.5, N_a=6, N_b=6, non-significant) and non-food objects (U=11.5, N_a=6, N_b=6, non-significant). In all food categories, for both species, the largest mean number of BV's was found within 30 seconds of the beginning of the trial (Figure 5.L), and the largest mean number of BV's found in non-food trials was less than the lowest value in food trials (for *S. labiatus* 0.6 vs. 1.2 : *S. fuscicollis* 0.7 vs. 0.8). This indicates that both species behaved as if they had an expectation of the presence of food in food object trials.

5.15 Experiment 5.2 B - Retention trials.

5.15.1 Introduction.

If the two species had gained any knowledge about the type of object, and they had some degree of "expectation" that food objects should contain food, then the monkeys should show more BV's in presentations of food objects, when compared to non-food objects. In experiment 5.2A, they were found to show this pattern on test trials, and as the food objects did not actually contain any food, any increased time spent upon the apparatus was thought to be due to an expectation of food and not merely a reaction to the presence of food itself.

In a set of previous studies, Menzel (1979) and Menzel & Juno (1982,1985) showed that tamarins would learn to react differently to repeated presentations of the same object, and could retain information about these objects over a period of time. The present study set out to test whether or not both species could retain their learning about the set of objects from experiment 5.2A, and whether the two species differed in their ability to do this.

5.15.2 Methods.

All six groups of both *S. labiatus* and *S. fuscicollis* from Experiment 5.2A were now tested on 2 presentations of food objects (F) and 2 presentations of non-food objects (NF) from phase II. The length of time between initial presentation and retention trials, varied between 13 and 54 days. The objects were presented to the subjects in isolation from each other and only one object was presented on each separate day. The objects were randomly presented (F or NF) in equal numbers in both the morning (0900-1230h) and the afternoon (1300-1630h). Different groups of subjects were presented the same objects at different times, to counteract possible order effects. Sample sessions and measures were identical to experiment 5.2A.

5.15.3 Results.

The two species were found to react differentially towards the two categories of objects (Figure 5. M [I]). Overall, both species had a significantly higher mean number of box visits (BV's) in food object categories, than in non-food categories ($T=21$, $N=6$, $p<0.05$). In both object types, the *S. labiatus* had a higher mean value of BV's, but this was not a significant different for either food ($U=7$, $N_a=6$, $N_b=6$, non-significant) or non-food objects ($U=7$, $N_a=6$, $N_b=6$, non-significant).

The tamarins both demonstrated a quicker mean approach and touch time for food objects (Figure 5.M [II + III]). Approach time was significantly quicker towards food objects for both *S. labiatus* ($T=21$, $N=6$, $p<0.05$), and *S. fuscicollis* ($T=19$, $N=6$, $p<0.05$). A similar pattern was found for mean latency to touch food objects, and this was again significantly quicker for both *S. labiatus* ($T=20$, $N=6$, $p<0.05$), and *S. fuscicollis* ($T=20$, $N=6$, $p<0.05$). The *S. labiatus* were quicker to react towards food objects than *S. fuscicollis*, but this difference was not significant for either approaching ($U=10$, $N_a=6$, $N_b=6$, non-significant) or touching ($U=15.5$, $N_a=6$, $N_b=6$, non-significant). On the other hand, *S. fuscicollis* had a quicker mean latency to respond to non-food objects, but once again this was not significantly different for either approaching or touching ($U=12$, $N_a=6$, $N_b=6$, non-significant).

The two species were shown to retain the increased response shown towards objects that were previously presented with food. Such food objects had a significantly greater number of BV's, and were approached and touched significantly quicker than non-food objects. Both species were therefore shown to retain information about the nature of an object. However, the two species did not significantly differ in their response to either the food or non-food objects, and so there is no evidence to suggest that either species was better than the other at retaining learning.

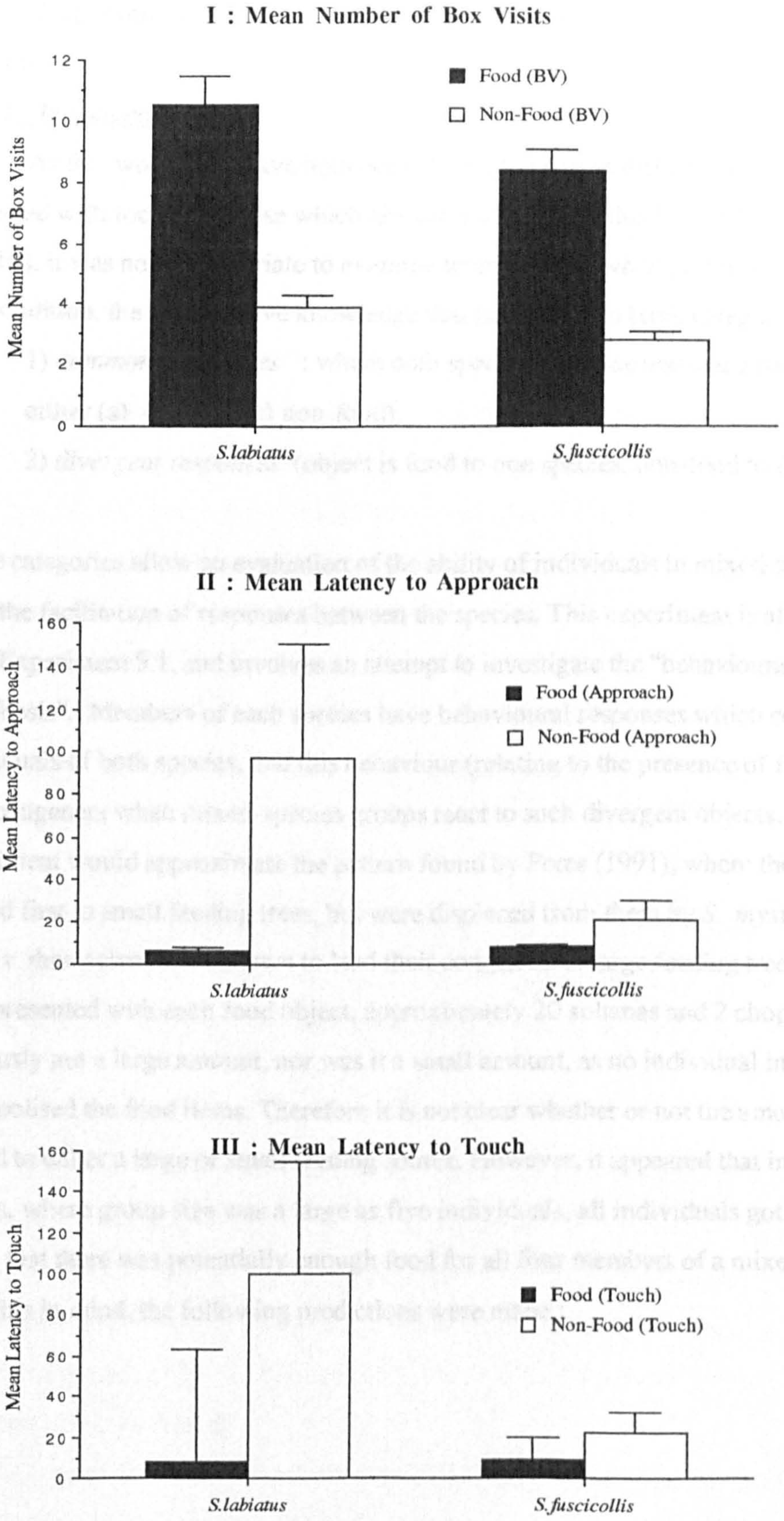


Figure 5.M : Mean number of box visits, latency to approach and touch, during retention trials.

5.16 Experiment 5.2 C : Mixed-species presentations of food and non-food objects.

5.16.1 Introduction.

As the two species have both been shown to learn to distinguish between objects that are presented with food, and those which are not, and to retain this information (Experiments 5.2A & 5.2B), it was now appropriate to examine their reaction when part of mixed-species groups. In this condition, the species have knowledge that falls into two basic categories ;

1) *common responses* : where both species have learned that a particular object is either (a) food, or (b) non-food).

2) *divergent responses* (object is food to one species, non-food to the other species).

These categories allow an evaluation of the ability of individuals in mixed-species groups to gain from the facilitation of responses between the species. This experiment is also an important step from Experiment 5.1, and involves an attempt to investigate the "behavioural facilitation hypothesis". Members of each species have behavioural responses which could benefit individuals of both species, and this behaviour (relating to the presence of food), is exposed to their congeners when mixed-species groups react to such divergent objects. It was hoped that this experiment would approximate the pattern found by Peres (1991), where the *S. fuscicollis* reacted first to small feeding trees, but were displaced from them by *S. mystax,* while the *S. mystax* themselves were shown to lead their congeners to large feeding trees. The amount of food presented with each food object, approximately 20 sultanas and 2 chopped cherries, was obviously not a large amount, nor was it a small amount, as no individual in any group monopolised the food items. Therefore it is not clear whether or not the amount of food could be related to either a large or small feeding source. However, it appeared that in the single species groups, where group size was a large as five individuals, all individuals got some food. This meant that there was potentially enough food for all four members of a mixed-species group. With this in mind, the following predictions were made :

1) Common responses

a) Food objects : the latency to contact the object and the number of animals in or around the box should be greatest in this category (although competitive exclusion by one species may occur).

b) Non-food objects : the latency to contact this object should be greater than in the above category and the number of individuals in/on the box should be lower.

2) Divergent responses : If they share knowledge about food resources then there should be a decrease in latency and increase in number of animals on apparatus in subsequent presentations, and the behaviour should be similar to other food objects.

In the divergent responses category, the behaviour of the tamarins and latency to contact the box will depend upon the facilitation of the responses of the species who have previously been presented with the object paired with food. If the behavioural response of the species who had previously learned that the object did not contain food now changed due to the reactions of the other species, then their behaviour has been facilitated due to the presence of these congeners. This is the type of facilitation that is being tested and in all categories of objects the behaviour of one species may be influenced by the dominance relationship between the two groups. As a consequence, any interactions between the species were noted.

5.17 Methods.

5.17.1 Subjects.

Five mixed-species groups (GP3, GP4, GP6, GP7 & GP8) were tested during this experiment. All had previously received a full set of monospecific object presentations (see above), and were tested in their own outdoor areas. Subjects were observed between June and August 1994.

5.17.2 Procedure.

Measures recorded were identical to the monospecific trials, but were carried out concurrently on both species. In addition, any competition between the species was noted (in categories from Section 3.7.10) and a count of the number of individuals present on the testing box immediately prior to the door being opened was also noted (recorded as number of individuals present in /on the box pre-trial). This pre-trial number was taken to indicate interest in the object being presented.

Competition was recognised to consist of any (a) aggressive behaviour (as defined in

Section 3.7.10) which led to the withdrawal of another individual, or (b) non-aggressive behaviour (i.e. approaching towards, or passing close by another) which also led to a withdrawal. However, both types of behaviour were actually scored as a "displacement". For the purposes of this study, a *displacement* is defined as ; any behaviour shown by of one or more individuals which leads directly to the withdrawal of one or more other individuals, regardless of whether or not it was accompanied by aggression. Displacements were noted when they occurred and the actor(s) and receiver(s) were recorded.

For the first part of the experiment, each mixed group was tested on 2 presentations of all phase II + III objects (from Experiment 5.2 A), where the second was a test presentation of the object itself. Objects were once again given in 2 phases, each containing random presentations of the 2 classes of previously encountered objects. **Phase II** *(a) Non-food Objects* [NF] - objects which never contained food for either species. *(b) Food Objects* [F] - objects that contained food for presentations to both species. **Phase III** *(a) Food / Non-Food Objects* [F(Sl) / NF(Sf)] - Objects that were presented with food for *S. labiatus* but never contained food for *S. fuscicollis*. *(b) Non-Food / Food Objects* [NF(Sl) / F(Sf)] - Objects that were never presented with food for *S. labiatus* but had contained food for *S. fuscicollis.*

In a second part of the experiment, the mixed groups were tested on 2 categories of new objects, (a) *Non-Food Objects* and (b) *Food Objects* (defined as above). All objects were novel to the group members of both species, and represented a chance to gauge the response of the mixed groups to the presence of new objects (see Appendix 2 foe list of objects).

Objects presented in section 1 (Phases **II** + **III**) were tested separately, followed by section 2 (new objects), with the previously used objects being tested initially, then the new ones. All objects were presented for two 10 minute sample sessions, the first containing food (if they were any of the three food object categories), the second was a test session containing no food. Again, the order of presentation was randomly varied and time of day was counterbalanced. Each group received only one sample session per day, and the second (test) sessions were carried out the day after initial presentation. All groups of other tamarins adjacent to the group being studied, were locked into their respective indoor areas, while the study group was locked out. The chosen object was placed into the testing box, and the door shut. The session began approximately 30 seconds later, when the door was opened to allow access to the object, and carried on for a period of 10 minutes.

5.18 Results.

5.18.1 Section 1 : "Known objects" : Phases II + III.

As both species received only two presentations of each object, the subsequent analysis was carried out on both these sessions, and the full data is shown in Appendix 5. Once again, it was decided to examine the results in terms of the two broad categories of data;
(a) differences within object categories, and (b) differences between categories of objects. These are examined separately.

5.18.2 Species differences within categories.

The species are compared on five different measures, i) the number of individuals pre-trial, ii) the mean number of box visits (BV's) per category, iii) the species of the first individual to enter the box, iv) the mean latency to enter box and successfully approach an object (< 15cm of object) and v) the mean latency to touch an object, in each category. All measures are compared per object category.

Mean number of subjects pre-trial.

The number of individuals present on the box before the trial began, was used to determine initial interest in the object. The two trials are examined separately, in order to determine differences in "expectations" between both species and between the various categories of objects (Figure 5.N). Table 5.W shows that the mean number of subjects on the box prior to the beginning of the sample period varied between the first and second (test) presentations. For *S. labiatus* there was no specific pattern and none of the presentations differed significantly. *S. fuscicollis* showed a general decrease on test presentations (Figure 5.N), but this reduction was only significant for Non-Food and Food / Non-Food [F(Sl) / NF(Sf)] objects (T=15, N=5, p<0.05).

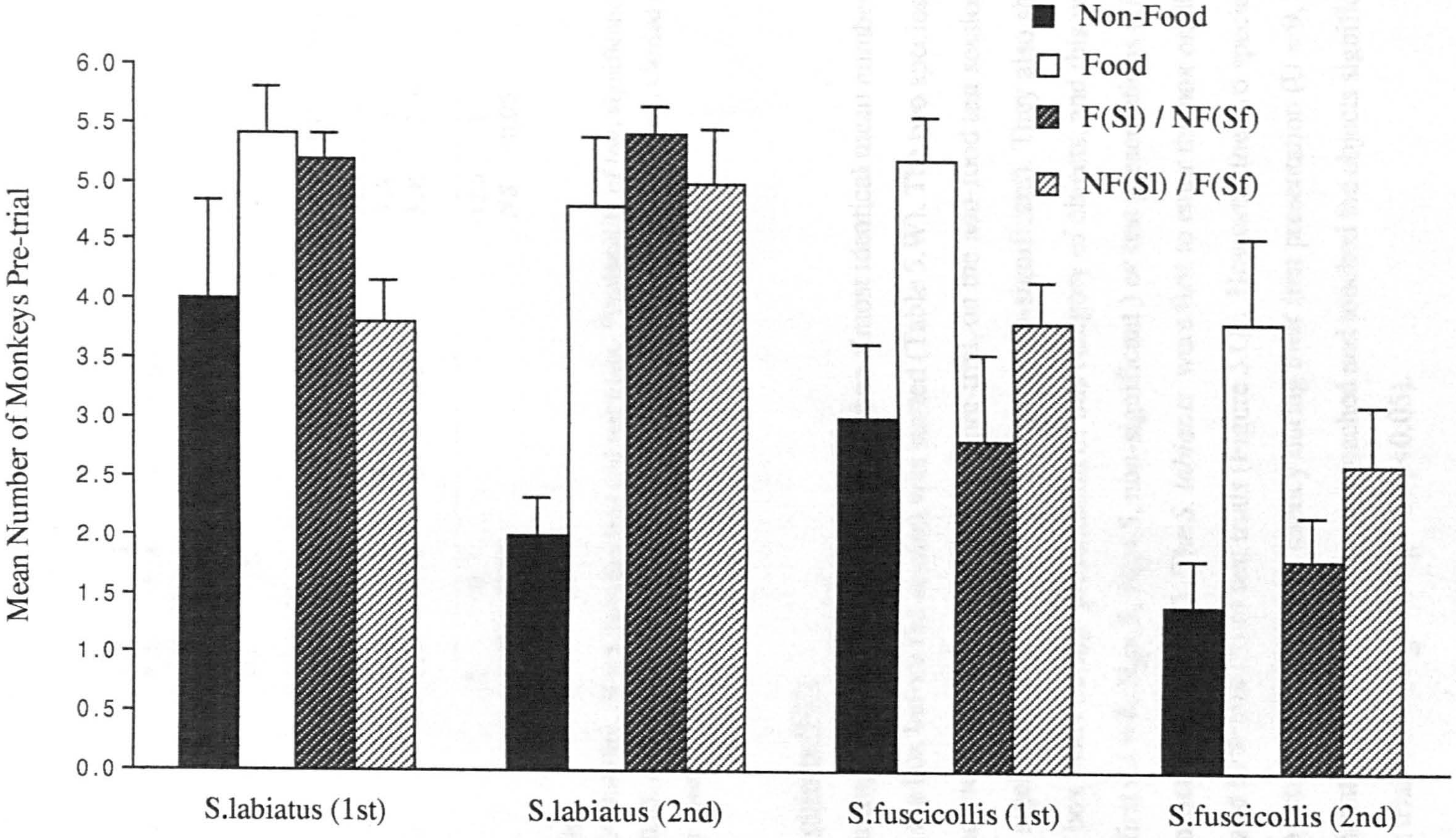


Figure 5.N : Mean number of monkeys on box prior to beginning of trial (Pre-trial number). Scores are amalgamated for 3 trials in each Category.

Table 5.W : Mean number of subjects on box pre trial, for five mixed-species groups of tamarins. Bold numbers refer to mean totals per group, summed over 3 trials per category.

	N / F				Food			
	1	2	WIL.^{1}	prob.^{2}	1	2	WIL.	prob.
S. labiatus	**4.0**	**2.0**	10	*NS*	**5.4**	**5.2**	4.5	*NS*
S. fuscicollis	**3.0**	**1.4**	15	< 0.05	**5.2**	**3.8**	10	*NS*
M-W^3	8	6.5			10.5	7.5		
probability	*NS*	*NS*			*NS*	*NS*		

	F(Sl) / NF(Sf)				NF(Sl) / F(Sf)			
	1	2	WIL.^{1}	prob.^{2}	1	2	WIL.	prob.
S. labiatus	**5.2**	**5.4**	4	*NS*	**3.8**	**5.0**	6	*NS*
S. fuscicollis	**2.8**	**1.6**	6	*NS*	**3.8**	**2.6**	15	<0.05
M-W	2	0			12.5	1		
probability	<0.05	<0.01			*NS*	<0.05		

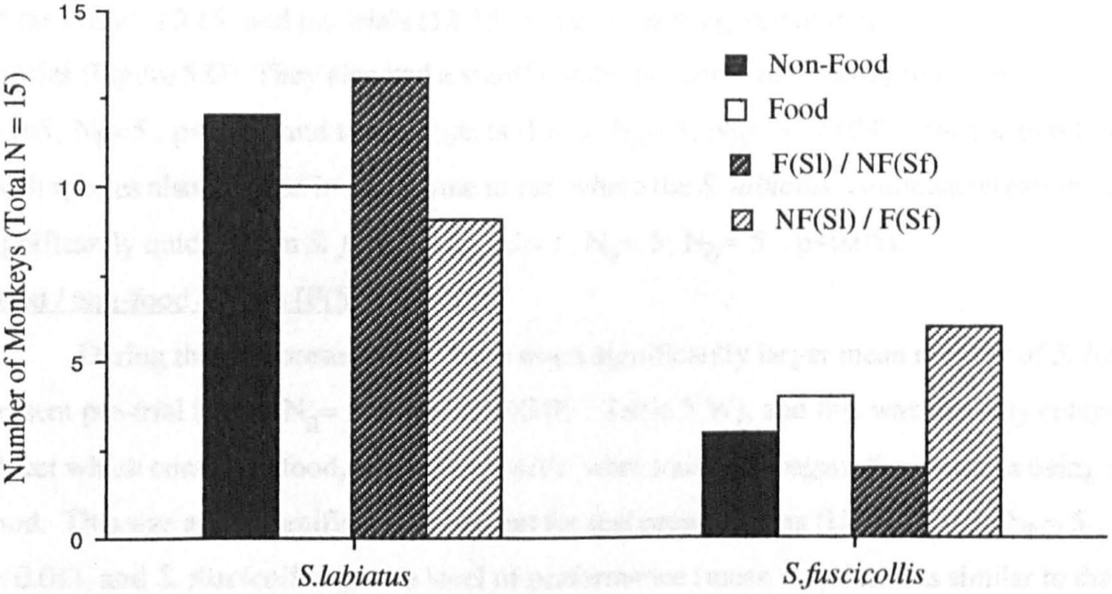
Notes

[1] Wilcoxon Probability, N = 5, between first and test trials. [2] Probability of test, significance level set at p=0.05. *NS* = non significant. [3] Mann-Whitney U-test, $N_a = 5$, $N_b = 5$. Carried out on total scores per species.

Non-food objects (NF)

During first trials, the two species had an almost identical mean number of subjects present on the box before the session was started (Table 5.W). The two species both had their smallest individual value of mean subjects pre-trial, on the non-food test sessions, but they did not differ significantly (U = 7.5, N_a= 5, N_b= 5, non-significant). They also showed a small number of box visits during presentation of this category of objects, and this was not different for either first (U = 6, N_a= 5, N_b= 5, non-significant) or test presentations (U = 8, N_a= 5, N_b= 5, non-significant : Table 5.X). The *S. labiatus* were first to enter the box on 80% (12/15) of the first trials and 67% (10/15) of test trials (Figure 5.O). However, the two species approached and touched objects in a similar mean latency during their first presentation (U = 9, N_a= 5, N_b= 5, non-significant), but the *S. labiatus* approached and touched the objects significantly quicker during test trials (U=4, N_a= 5, N_b= 5, p<0.05).

I : First Trials



II : Test Trials

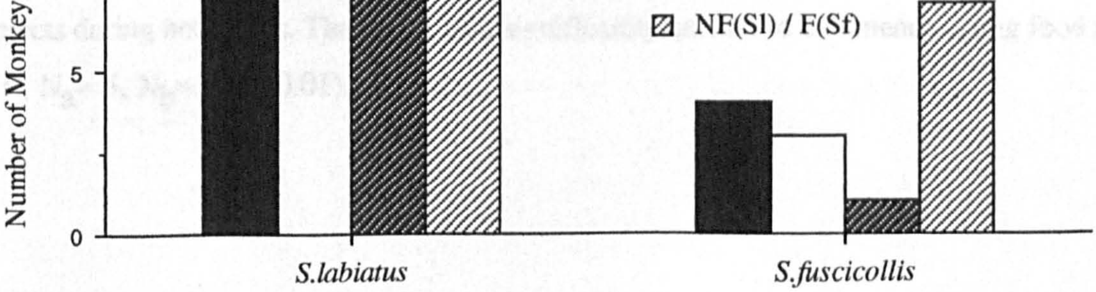


Figure 5.O : First individual to enter box during mixed-species trials.

Food objects.

There was a specific pattern found, with *S. labiatus* showing a larger mean pre-trial number on the box, for both trials, but this was not significantly greater (Table 5.W). The two species had a similar mean number of box visits (BV's) during the first presentation of food objects, but by the test trial, the *S. labiatus* had a significantly greater mean number of BV's ($U = 2.5$, $N_a = 5$, $N_b = 5$, $p < 0.05$: Table 5.X). The *S. labiatus* were first to enter the box on most of the initial (10/15) and test trials (12/15), which may suggest that they were the more dominant species (Figure 5.O). They also had a significantly quicker mean latency to approach ($U = 1$, $N_a = 5$, $N_b = 5$, $p < 0.05$) and touch objects ($U = 2$, $N_a = 5$, $N_b = 5$, $p < 0.05$) for the two trials. Both species also differed in mean time to eat, where the *S. labiatus* commenced eating the food significantly quicker than *S. fuscicollis* ($U = 1$, $N_a = 5$, $N_b = 5$, $p < 0.05$).

Food / non-food objects [F(Sl) / NF(Sf)]

During the first presentation, there was a significantly larger mean number of *S. labiatus* present pre-trial ($U = 2$, $N_a = 5$, $N_b = 5$, $p < 0.05$: Table 5.W), and this was the only category of object which contained food, but *S. fuscicollis* were trained to regard the object as being non-food. This was again significantly different for test presentations ($U = 0$, $N_a = 5$, $N_b = 5$, $p < 0.01$), and *S. fuscicollis* gave a level of performance (mean 1.6) that was similar to that of non-food (NF) objects (mean 1.4).

The two species had a similarly sized mean number of BV's during first trials, and so did not differ significantly ($U = 9.5$, $N_a = 5$, $N_b = 5$, non-significant). In the test trials, the two species again had no significant difference ($U = 10$, $N_a = 5$, $N_b = 5$, non-significant). However, as would be expected in the F(Sl) / NF(Sf) category, where *S. labiatus* were the only species which had learned about the presence of food, they were the first to enter the box on almost every session (87%, 13/15). They were subsequently shown to be significantly quicker to both approach ($U = 0$, $N_a = 5$, $N_b = 5$, $p < 0.01$) and touch ($U = 1$, $N_a = 5$, $N_b = 5$, $p < 0.05$) such objects during both trials. They were also significantly quicker to commence eating food items ($U = 0$, $N_a = 5$, $N_b = 5$, $p < 0.01$).

Table 5.X : Mean number of box visits (BV's), latency to approach, touch and eat in five mixed-species groups of tamarins. Bold numbers refer to mean totals per group summed over 3 objects per category, while standard errors are bracketed.

I : Mean number of BV's

	S. labiatus		*S. fuscicollis*	
	1	Test	1	Test
Food	**15.3** (1.2)	**7.3** (0.5)*	**16.9** (2.1)	**5.0** (0.6)*
Non-Food	**4.5** (0.6)	**2.1** (0.3)*	**3.6** (1.1)	**3.0** (0.6)*
F(Sl) / NF(Sf)	**14.0** (1.2)	**6.6** (0.4)*	**16.1** (1.7)	**7.0** (0.7) *
NF(Sl) / F(Sf)	**12.7** (1.2)	**7.1** (0.9)*	**12.6** (0.7)	**6.5** (0.5)*

II : Mean latency to approach.

	S. labiatus		*S. fuscicollis*	
	1	Test	1	Test
Food	**6.8** (1.1)	**7.9** (2.4)	**34.5** (17.5)	**33.0** (10.1)
Non-Food	**60.7** (26.6)	**49.1**(17.8)	**73.2** (15.3)	**120.2** (35.3)
F(Sl) / NF(Sf)	**4.9** (0.9)	**5.4** (0.9)	**42.2** (18.3)	**26.3** (10.9)*
NF(Sl) / F(Sf)	**7.7** (1.1)	**8.7** (3.2)	**26.6** (10.3)	**44.1** (13.4)

III : Mean latency to touch.

	S. labiatus		*S. fuscicollis*	
	1	Test	1	Test
Food	**8.4** (1.3)	**8.9** (2.5)	**40.1** (18.0)	**34.8** (10.0)
Non-Food	**62.3** (26.9)	**50.2**(17.8)	**76.0** (14.2)	**121.3** (35.3)
F(Sl) / NF(Sf)	**5.8** (0.9)	**6.3** (0.9)	**43.2** (18.3)	**27.6** (10.9)*
NF(Sl) / F(Sf)	**8.7** (1.2)	**9.8** (3.1)	**27.2** (10.3)	**45.3** (13.2)

IV : Mean latency to eat food item.

	S. labiatus		*S. fuscicollis*	
	1	Test	1	Test
Food	**10.0** (1.2)	-	**61.0** (33.6)	-
Non-Food	-	-	-	-
F(Sl) / NF(Sf)	**7.1** (0.9)	-	**44.1** (18.4)	-
NF(Sl) / F(Sf)	**10.7** (1.7)	-	**28.5** (10.4)	-

Note

*** Significance on Wilcoxon Test , N = 5, between first and test trials. Significance level set at p=0.05.**

Non-food/ food objects [NF(Sl) / F(Sf)]

The test presentation had a significantly larger mean number of *S. labiatus* present pre-trial, in the NF(Sl) / F(Sf) object category (U= 1, N_a= 5, N_b= 5 , $p<0.05$). This result was interesting, as *S. labiatus* were trained to regard these objects as "non-food" and in the first presentation showed a mean number of individuals (3.8) similar to that for first presentation of NF objects (4), and identical to that of *S. fuscicollis* (Table 5.W). This was confirmed by the highest incidence of *S. fuscicollis* entering the box first, of any of the object categories (Figure 5.O). They were first to enter on 40% (6/15) of first trials, and 47% (7/15) of test trials. On the test presentation, the pre-trial number of *S. labiatus* had increased to an amount similar to the other "food" categories, while the *S. fuscicollis* decreased. There was no corresponding rise for *S. fuscicollis* in the F(Sl) / NF(Sf) category. This suggests that the response of *S. labiatus* may be changed by the behaviour of their congeners (i.e. the initial entry to the box by *S. fuscicollis*), and by the test presentation they were reacting to these objects as "food" objects.

Both *S. labiatus* and *S. fuscicollis* had a similar mean amount of BV's during first trials (U = 11.5, N_a= 5, N_b= 5, non-significant) and test trials (U = 11, N_a=5, N_b=5, non-significant). They also did not differ significantly in mean latency to approach, touch and eat, during the first trials (U = 8, N_a= 5, N_b= 5, non-significant). However, by the test trials, the *S. labiatus* were both approaching and touching the objects significantly quicker than the *S. fuscicollis* (U = 2, N_a= 5, N_b= 5, $p<0.05$).

5.18.3 Differences between the categories.

The two species were compared separately, comparing and contrasting the performance shown towards the four object categories. There was found to be differences between the two trials, the number of subjects on the box pre-trial, the mean BV's per individual, the mean approach time, the mean touch time, and the first animal to encounter the object (Table 5.X).

Mean number of subjects pre-trial.

The amount of animals that were present pre-trial were compared between the non-food and the three food categories. Figure 5.N shows that the mean number of animals present on the box changed for both species, over categories. The initial level of response was related to the nature of the objects ; those that were "food" objects (F & F(Sl) / NF(Sf) for *S. labiatus* ; F & NF(Sl) / F(Sf) for *S. fuscicollis*) had a similar number of animals pre-trial, as did the two categories containing <u>"non-food" objects</u> (NF & NF(Sl) / F(Sf) for *S. labiatus* ; NF & F(Sl) / NF(Sf) for *S. fuscicollis*). This increased amount of responding can probably be related to an initial "expectation" of food, gained through prior training. However, in *S. labiatus* the mean amount of animals present on the box during the first presentations were only significantly different between F & NF(Sl) / F(Sf) object categories (Table 5.Y).

Table 5.Y : Pairwise analysis of mean total number of individuals pre-trial, mean number of box visits, mean approach and touch. All are compared between first and test presentations of all 4 categories of food and non-food objects. Bold figures are Wilcoxon test scores.

S. labiatus	Pre-trial		Mean BV		Approach		Touch	
	1	2	1	2	1	2	1	2
F vs. NF [1]	**13**	**15***	**15***	**15***	**15***	**14***	**15***	**14***
F vs. NF(Sl) / F(Sf)	**14***	**4**	**11**	**8**	**10**	**10**	**10**	**9**
F vs. N(Sl) / NF(Sf)	**4**	**6**	**8**	**12**	**11.5**	**11**	**13**	**11**
NF vs. F(Sl) / NF(Sf)	**8.5**	**15***	**15***	**15***	**15***	**15***	**15***	**15***
NF vs. NF(Sl) / F(Sf)	**8.5**	**15***	**15***	**15***	**10**	**15***	**14***	**15***
F(Sl) / NF(Sf) vs. NF(Sl) / F(Sf)	**10**	**7.5**	**10**	**9.5**	**15***	**10**	**15***	**10**

S. fuscicollis	Pre-trial		Mean BV		Approach		Touch	
	1	2	1	2	1	2	1	2
F vs. NF [1]	**15***	**15***	**15***	**15***	**12**	**14***	**12**	**14***
F vs. NF(Sl) / F(Sf)	**10**	**13.5**	**14***	**15***	**9**	**11**	**10**	**11**
F vs. F(Sl) / NF(Sf)	**10**	**9**	**8**	**13**	**11**	**6**	**10**	**10**
NF vs. F(Sl) / NF(Sf)	**2**	**4.5**	**15***	**15***	**12**	**15***	**12**	**15***
NF vs. NF(Sl) / F(Sf)	**8.5**	**10**	**15***	**15***	**14***	**14***	**14***	**14***
F(Sl) / NF(Sf) vs. NF(Sl) / F(Sf)	**6**	**6**	**14***	**10**	**12**	**14***	**12**	**14***

<u>**Notes**</u>

NF = Non Food objects, F = Food objects, F(Sl) / NF(Sf) = Food objects for *S. labiatus*, non-food objects for *S. fuscicollis*. NF(Sl) / F(Sf) = Non-food objects for *S. labiatus*, food objects for *S. fuscicollis*.

*** Significant difference on Wilcoxon Test at p=0.05, Where N= 5, all other scores were non-significant.**

This was despite the general pattern of responses to the three categories which had been paired with food having more monkeys present pre-trial. In the test trial, all three object categories which had been paired with food [i.e. F. NF(Sl) / F(Sf), F(Sl) / NF(Sf)] were found to have a significantly greater mean number of *S. labiatus* present prior to the trial, when compared to the NF category (T=15, N=5, $p<0.05$). This confirms that the NF(Sl) / F(Sf) objects were now being regarded as containing food by the *S. labiatus.* For *S. fuscicollis*, the pattern was not the same, and the only significant differences were that there were a greater mean number of monkeys present pre-trial in the two food (F) trials, when compared to the non-food (NF) trials (T=15, N=5, $p<0.05$). All other pairings were found not to differ significantly from each other (Table 5.Y).

<u>The first animal to enter box.</u>

There was a strong pattern of *S. labiatus* being first to enter the box on most trials (Figure 5.O). They were found to enter 73% of first presentation and 72% of test presentation trials before the *S. fuscicollis.* They entered the box during the NF, Food and F(Sl) / NF(Sf) trials before the *S. fuscicollis*, doing so on at least 66% of trials (NF) and up to 87% (F(Sl) / NF(Sf)). This highest level was on the category where *S. labiatus* was regarding the object as a "food" object, while *S. fuscicollis* was regarding it as non-food. It was reasonable to assume that *S. fuscicollis* did not regard this as food, because they had few animals present on the box pre-trial (Table 5.W). On the NF(Sl) / F(Sf) objects, where the opposite training was supplied to the species, the *S. fuscicollis* had their highest number of "first to enter" scores during any category, and were first to enter on some 40% of first and 47% of test trials. As outlined above, the *S. labiatus* had a low number of pre-trial subjects present during initial presentations.

Overall, this suggests that the *S. labiatus* were generally first to enter the box, and that this entry may be related to an expected presence of food items. The straightforward conclusion is that *S. labiatus* may be more dominant, or superior in retaining information concerning objects, to *S. fuscicollis.* However, the former is likely to be the case, as both *S. labiatus* and *S. fuscicollis* had their largest number of "first entries" during the divergent response categories. This is where the associating species would only realise that food was present after the initial reaction of their congeners.

Mean number of box visits.

For *S. labiatus,* all test presentation trials significantly differed from first presentations (T=15, N=5, p<0.05 : Table 5.X). In *S. fuscicollis,* Food, F(Sl) / NF(Sf) and NF(Sl) / F(Sf) objects all had a significant difference between the mean number of BV's on the two trials (T=15, N=5, p<0.05), while the two presentations of Non-food objects were not significantly different (T=10, N=5, non-significant).

Both *S. labiatus* and *S. fuscicollis* had a significantly larger mean number of box visits during both trials of food (F) objects compared with non-food objects (T=15, N=5, p<0.05). The *S. labiatus* did not have a significant difference between the mean BV's shown towards Food (F) objects and that shown to both divergent status objects (i.e.NF(Sl) / F(Sf) and F(Sl) / NF(Sf)). This pattern was found during both trials (Table 5.Y). However, these two objects had a significantly greater mean number of of BV's when compared to NF objects (T=15, N=5, p<0.05). The same pattern was found between NF and divergent objects in *S. fuscicollis* (T=15, N=5, p<0.05). However, while the mean number of BV's shown towards food objects was not significantly different to that of F(Sl) / NF(Sf) (i.e. non-food for *S. fuscicollis*), it was significantly greater than that in the NF(Sl) / F(Sf) during first trials (T=14, N=5, p<0.05) , but significantly smaller during test trials (T=15, N=5, p<0.05). This category was where *S. fuscicollis* had the prior experience of the object containing food, and these results probably reflect this advantage for them.

Mean latency to approach.

In all three categories[F, F(Sl) / NF(Sf), NF(Sl) / F(Sf)], in which objects had previously been paired with food, the *S. labiatus* approached objects significantly quicker than NF objects, when compared on test trials with no food (Table 5.Y). They also approached the first (training) presentation trials of the two categories of objects in which single species groups of *S. labiatus* had been presented with food (F & F(Sl) / NF(Sf)) significantly quicker (T=15, N=5, p<0.05). In NF(Sl) / F(Sf) objects, which were previously presented without food, they were not approached significantly quicker on first trials (T=10, N=5, non-significant). The *S. labiatus* had a broadly similar mean latency to approach all of the three object categories which had been paired with food, and the two divergent learning categories were not significantly different from the Food category (Table 5.Y). The mean latency to approach F(Sl) / NF(Sf) objects was the quickest overall on both trials. The initial reaction to these two categories was different and during first trials F(Sl) / NF(Sf) objects were approached in a significantly quicker mean latency than NF(Sl) / F(Sf) objects ($T=15$, $N=5$, $p<0.05$), but by the test trial they did not differ significantly ($T=10$, $N=5$, non-significant).

In test trials containing no food for *S. fuscicollis*, the latency to approach objects in the three categories which had been previously paired with food, was quicker than that given to objects in the NF category (Table 5.X). This difference was only significant when comparing NF(Sl) / F(Sf) with NF objects during the first trial ($T=14$, $N=5$, $p<0.05$). When tested on trials not containing any food, the mean latency to approach was significantly faster, when comparing the three categories of objects previously paired with food, against NF objects (Table 5.Y). None of these three food paired categories differed from each other during initial trials, but in the NF(Sl) / F(Sf) category, where *S. fuscicollis* had the initial advantage over *S. labiatus* they had their quickest mean approach time for any category. The F(Sl) / NF(Sf) objects were approached significantly quicker than NF(Sl) / F(Sf) categories during test trials ($T=14$, $N=5$, $p<0.05$).

Mean latency to touch.

As touches occurred shortly after approach, for *S. labiatus*, the pattern of mean touch time was similar to approach time (Table 5.X). Once again, all three categories of objects which had been previously paired with food, were touched significantly quicker than non-food objects, during both first and test trials (Table 5.Y). The F(Sl) / NF(Sf) category was touched significantly quicker than the NF(Sl) / F(Sf) category on the first trial ($T=15$, $N=5$, $p<0.05$), but by the test trial there was no significant difference ($T=10$, $N=5$, non-significant).

For *S. fuscicollis* the pattern of touches was identical to approaches (Table 5.X). During first trials, only the NF(Sl) / F(Sf) category was touched significantly quicker than the non-food objects ($T=14$, $N=5$, $p<0.05$), again suggesting that in this category the *S. fuscicollis* had an advantage over their congeners. During test trials, all three categories of objects which were previously paired with food, were now touched significantly quicker ($T=14$, $n=5$, $p<0.05$). The NF(Sl) / F(Sf) category was touched quicker than the F(Sl) / NF(Sf) category in the first trial, but this was not significant ($T=10$, $N=5$, non-significant). However, in the test trial, the opposite pattern was found, and the F(Sl) / NF(Sf) objects were touched significantly quicker ($T=14$, $N=5$, $p<0.05$).

Summary of the reaction to the various categories of objects.

The two species had similar amounts of box visits for most categories, and had a similar number of animals pre-trial for the NF and F categories. *S. labiatus* were significantly quicker on both trials, to approach and touch the objects, and to gain food items from them (F & F(Sl) / NF(Sf)). On categories where they were not expecting food (i.e. NF & NF(Sl) / F(Sf)), the *S. labiatus* did not have significantly more subjects pre-trial, nor did they approach, touch and eat the objects significantly quicker than *S. fuscicollis.* However, by the test trials, there were significantly more *S. labiatus* on the box during NF(Sl) / F(Sf) objects, and they approached and touched objects significantly quicker.

Both species reacted to objects according to the presence or absence of food items, and also to the "expectation" of them. In test trials, both species exhibited significantly more animals pre-trial, significantly more box visits and a quicker mean approach and touch time towards Food objects, when compared to NF objects. This occurred, even though all test trials contained no food items. Neither species had any significant differences between F and F(Sl) / NF(Sf) objects. However, in NF(Sl) / F(Sf) objects, which were initially a "food" category for *S. fuscicollis,* and a "non-food" category for *S. labiatus*, the latter had significantly less subjects present pre-trial during first trials. The *S. fuscicollis* had a significantly lower mean number of BV's on test trials, when comparing NF(Sl) / F(Sf) with F categories. The *S. fuscicollis* also had their largest number of "first to enter box" scores on the NF(Sl) / F(Sf) category. On the three other categories, *S. labiatus* were first to enter on most occasions.

The two species also had significantly more BV's, and were quicker to approach and touch both divergent categories (i.e. F(Sl) / NF(Sf), NF(Sl) / F(Sf)), during test trials, when compared to the NF category. This shows that these objects were now regarded as food objects by both species. The two species had their quickest mean approach and touch times on the first trials of their "divergent" food categories. This indicates that the initial expectation of food by only one species allowed that species to gain quicker access to these resources. The *S. labiatus* also had significantly more subjects present pre-trial, on both these categories. For *S. fuscicollis*, the number of BV's shown towards first trial NF(Sl) / F(Sf) objects, was significantly greater than that given towards F(Sl) / NF(Sf) objects, but these in turn were approached and touched significantly quicker. *S. labiatus* only differed between these object categories, in mean latency to approach and touch objects on the first trials, as by the test trials they reacted to both categories as if they were "food" objects.

5.18.4 Box visits over the first 2.5 minutes.

As the *S. fuscicollis* were generally slower to approach and touch objects than *S. labiatus*, except in the category where they had the "expectation" of food, and *S. labiatus* did not (i.e. NF(Sl) / F(Sf)), it was decided to compare the number of box visits over the first 2.5 minutes, to look for patterns. As the presence of food was a factor in the first trials, only the test trials are compared (Figure 5.P).

In the two categories paired with food for single-species groups of *S. labiatus* (i.e. F, F(Sl) / NF(Sf)), there was a larger mean number of them present on the box for approximately the first 75 seconds. A similar pattern was found for the NF objects. This suggests that the *S. fuscicollis* were perhaps slower to respond to the objects, or had a lesser response. However, as the two species did not have a significantly different mean number of box visits, then the overall response was similar. Also, the category where *S. fuscicollis* had prior learning about the presence of food (NF(Sl) / F(Sf)), showed that the pattern was not simply a slower response, as they had a larger mean number of subjects present between 30 and 75 seconds. The position was thought to be related to dominance, and this is examined below.

5.18.5 Interactions during trials.

Interactions were recorded where and when they occurred, and are reported as mean totals per group (Table 5.Z). From this, it is clear that *S. labiatus* had priority in recorded interactions, as they were the more dominant in 99% (208/ 210) of interactions. There was a clear patterning of under which categories interactions occurred, where only 7.7% (16 / 210) were found during presentations which contained no food items, even though such presentations accounted for over 43% of all trials. This suggests that displacements were competition between the species, for access to food. It was clear these interactions were mostly non-aggressive displacements, accounting for some 81.4% (171/210) of all interactions, and represent competition between the species.

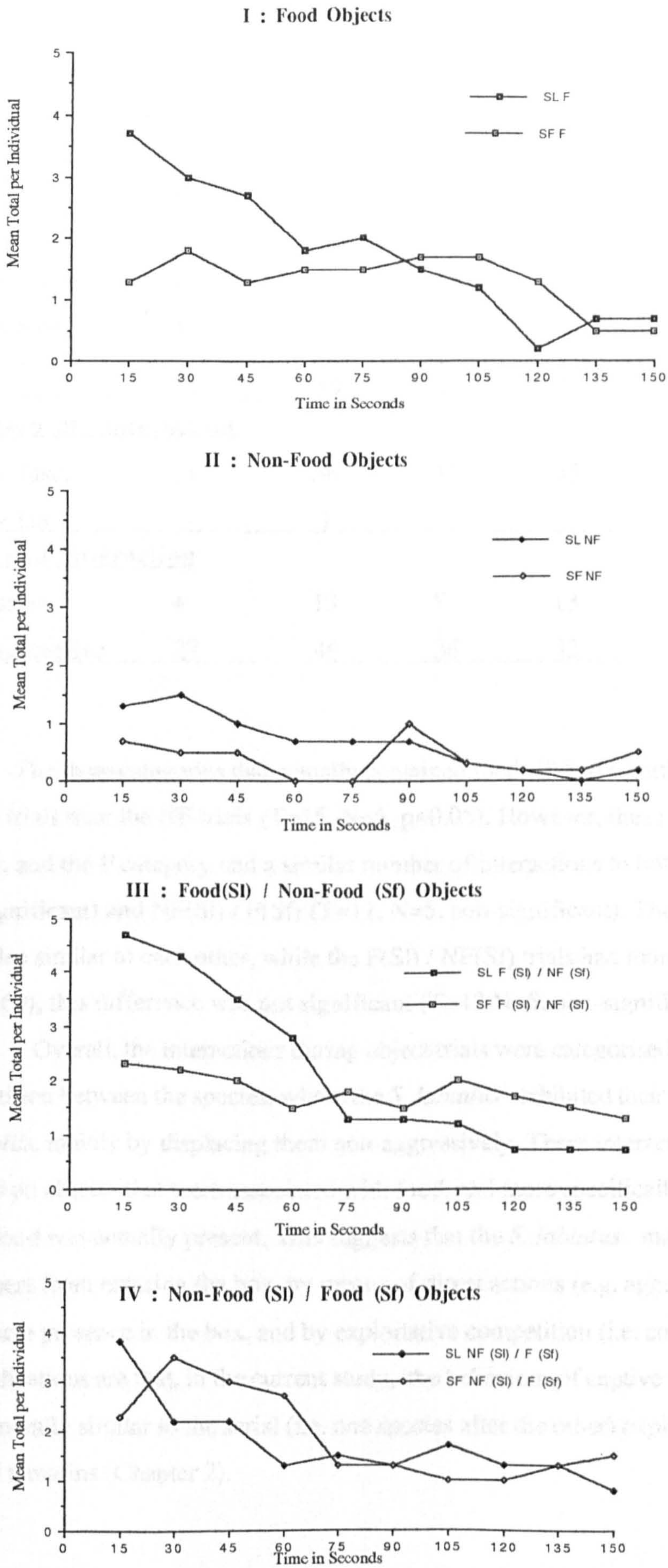


Figure 5.P : Mean number of box visits over the first 2.5 minutes of mixed-species test trials.

Table 5.Z : Occurrence, direction, and nature of interactions between the species, in mixed-species food and non-food trials.

	GP3	GP4	GP6	GP7	GP8	Total
Category						
Food Present	27	54	39	42	32	194
Food Absent	4	5	2	3	2	16
Total	31	59	41	45	34	210
Direction of interaction						
Lab. > fusc.	31	58	40	45	34	208
Fusc. > lab	-	1	1	-	-	2
Nature of Interaction						
Aggressive	4	13	5	13	4	39
Non-Aggressive	27	46	36	32	30	171

The three categories that actually contained food, all had significantly more interactions during trials than the NF trials (T=15, N=5, $p<0.05$). However, these three categories were very similar, and the F category had a similar number of interactions to both F(Sl) / NF(Sf) (T=8, N=5, non-significant) and NF(Sl) / F(Sf) (T=11, N=5, non-significant). These two divergent categories were also similar to each other, while the F(Sl) / NF(Sf) trials had more interactions during them (76 vs 60), this difference was not significant (T=12,N=5, non-significant).

Overall, the interactions during object trials were categorised as being a form of competition between the species, where the *S. labiatus* exhibited their ability to dominate the *S. fuscicollis*, mainly by displacing them non-aggressively. These interactions were predominantly centred on objects that were associated with food, and more specifically were shown mainly when food was actually present. This suggests that the *S. labiatus* may be excluding their congeners from entering the box, by means of direst actions (e.g. aggression, displacements), by their mere presence in the box, and by exploitative competition (i.e. consuming the food items). The indications are that, in the current study, the behaviour of captive mixed-species tamarins was generally similar to the serial (i.e. one species after the other) exploitation of resources found in wild tamarins (Chapter 2).

5.18.6 Comparison of single- and mixed-species test trials.

Both species were compared on their performance on test trials in both single-species and mixed-species groups, in order to investigate how performance for all four object categories had changed between the two conditions.

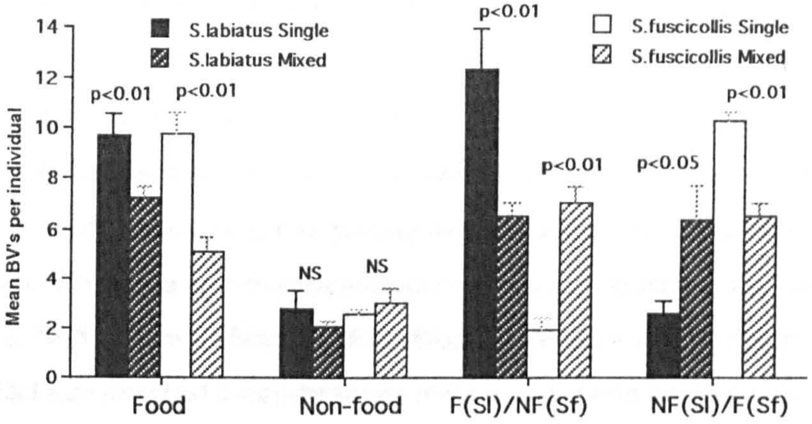
Box visits.

Both species had a significant reduction in mean number of box visits (BV) shown to Food objects during mixed-species test trial trials, when compared with single-species test trials (both T =15, N=5, $p<0.01$). There were no significant differences in BV's shown towards Non-food objects for either *S.labiatus* (T =9, N=5, non-significant) or *S.fuscicollis* (T =8.5, N=5, non-significant). Therefore, both species showed a similar pattern of behaviour towards these two common status object types (Food objects & Non-food objects) in single and mixed-species trials. However, in objects which only single-species groups of *S.labiatus* were presented with food (F(Sl) / NF(Sf)), an opposing pattern was found for each species (see Figure 5.Q [I]). *S.labiatus* had a significant reduction (T =15, N=5, $p<0.01$) in mean number of BV's in mixed-species trials, while *S.fuscicollis* had a significant increase (T =15, N=5, $p<0.01$). In objects with which only single-species groups of *S.fuscicollis* were presented with food (NF(Sl) / F(Sf)), a similar pattern was found where the two species had the opposite response (see Figure 5.Q [I]). However, this time *S.fuscicollis* had a significant decrease in performance (T =15, N=5, $p<0.01$), while *S.labiatus* had a significant increase (T =14, N=5, $p<0.05$). These results suggest that in the two divergent conditions, the behaviour of the species which were initially trained to associate food with the objects in single-species trials, brought about a change in behaviour in the associating species, by alerting them to the presence of food through social facilitation.

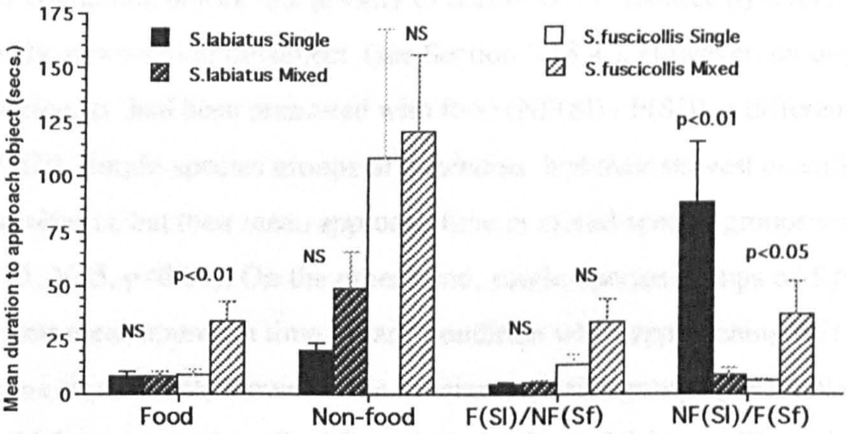
Mean latency to approach objects.

S.labiatus had priority of access to food objects (see Section 5.18.4), and it was clearly shown that they had a similar latency to approach food objects in both conditions (T=7, N=5, non-significant), while *S.fuscicollis* had a significantly slower latency to approach food objects in mixed-species trials (T=15, N=5, $p<0.01$). Both species had a slower mean latency to approach Non-food objects in mixed-species trials, but this was not significant for either *S.labiatus* (T=13, N=5, non-significant) or *S.fuscicollis* (T=8, N=5, non-significant). However, once again the divergent conditions showed that the behaviour in mixed-species groups was dependent upon

(I) Box visits per individual



(II) Mean latency to approach object



(III) Mean duration to touch object

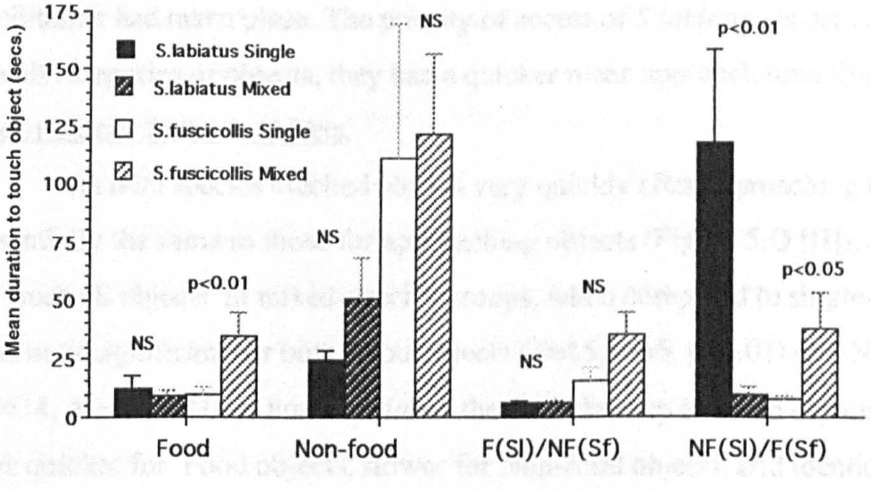


Figure 5.Q : Comparison of box visits (BV's), mean duration to approach and touch objects in single and mixed-species test trials. Scores are mean values, with standard error bars.

Significance on Wilcoxon Test shown above bars.

social facilitation of food resources and priority of access to these resources (Table 5.Q [II]). This is because in objects where only single-species groups of *S.labiatus* had been presented with food, they behaved in a manner similar to that shown to Food objects. Specifically, *S.labiatus* were not significantly quicker to approach F(Sl) / NF(Sf) objects in mixed-species trials (T=14, N=5, p<0.05), which is not surprising as these are always food objects for this species. The *S.fuscicollis* had a non-significant increase in mean latency to approach F(Sl) / NF(Sf) objects (T=12, N=5, non-significant) and in effect reacted in a similar manner as they did to Food objects. The fact that they had a significant increase in mean number of BV's for this object in mixed-species groups, demonstrates that although they now reacted to this object in the same way as a food-containing object, the priority of access to the resource by *S.labiatus* prevented them from quickly approaching the object (see Section 5.18.4). However, on objects where only *S.fuscicollis* had been presented with food (NF(Sl) / F(Sf)), a different pattern emerged (Figure 5.Q [II]). Single-species groups of *S.labiatus* had their slowest overall mean approach latency for these objects, but their mean approach time in mixed-species groups was significantly quicker (T=15, N=5, p<0.01). On the other hand, single-species groups of *S.fuscicollis* had their quickest mean approach time for any condition when approaching NF(Sl) / F(Sf) objects, but this became significantly slower when in mixed-species groups (T=14, N=5, p<0.05). This suggests that *S.labiatus* have benefited from the behaviour of *S.fuscicollis*, which were trained to regard these objects as containing food, and that their mixed-species performance shows that social facilitation had taken place. The priority of access of *S.labiatus* is demonstrated by the finding that for all categories of objects, they had a quicker mean approach time (Figure 5.Q).

Mean latency to touch objects.

As both species touched objects very quickly after approaching them, the results are essentially the same as those for approaching objects (Figure 5.Q [II]). *S.fuscicollis* were slower to touch all objects in mixed-species groups, when compared to single-species groups, but this was only significant for both Food objects (T=15, N=5, p<0.01) and NF(Sl) / F(Sf) objects (T=14, N=5, p<0.05). For *S.labiatus*, the mean latency to touch objects in mixed-species groups was quicker for Food objects, slower for Non-food objects, and identical for F(Sl) / NF(Sf) objects, but all were non-significant (T's =12, 12, 7.5 respectively, N=5, non-significant). The only significant difference was the *S.labiatus* were quicker to touch NF(Sl) / F(Sf) objects in mixed-species groups (T=14, N=5, $p<0.05$). Overall, the significant differences were identical to those for approaches and they support the notion that the behaviour of *S.fuscicollis* had influenced the behaviour of *S.labiatus* and that the *S.labiatus* could gain a greater benefit from the actions of their congeners, due to their priority of access to food (Figure 5.Q).

5.19 Section 2 : Novel food & non-food objects.

5.19.1 Food vs non-food objects.

The two species were now presented with a new set of three novel objects which were paired with food, and three different ones which were not. This was an opportunity to examine how the mixed-species group as a whole reacted to new objects. The full set of results are presented in Appendix 6.

Number of animals pre-trial.

The two species did not significantly differ in the mean number of subjects they had on the testing box pre-trial, when comparing food and non-food objects (Table 5.AA). They also did not differ significantly in the number of subjects on both trials, even though the mean number reduced on test trials. The two species did not differ in the pre-trial number of subjects that they had on the box during food objects, for either first trials (U=5.5, N_a=5,N_a=5, non-significant) or test trials (U=9, N_a=5,N_a=5, non-significant). However, the *S. labiatus* had more subjects present in all categories, and this difference was significant for first trials of NF objects (U=1.5, N_a=5,N_a=5, $p<0.05$), but was not significant for test trials (U=9, N_a=5,N_a=5, non-significant).

Mean number of box visits.

This measure demonstrated that both species had a significantly greater number of subjects present during first trials, and that for both presentations there were more subjects of each species present during food trials (T=15, N=5, $p<0.05$: Table 5.Z). This difference was apparent over the first 2.5 minutes of test trials, where both species had more individuals present during objects which had been paired with food (Figure 5.R). The two species had a similar number of first trial box visits (BV's) during both food paired objects (U=7.5, N_a=5,N_a=5, non-significant) and non-food objects (U=12.5, N_a=5, N_a=5, non-significant). There were significantly more *S. labiatus* BV's during the food trials (U=2, N_a=5,N_a=5, $p<0.05$), but the two species did not differ in non-food trials (U=6, N_a=5, N_a=5, non-significant).

Table 5. AA : Mean number pre-trial, number of box visits (BV's), latency to approach, touch and eat during novel food paired and non-food objects. Bold numbers refer to mean totals per group summed over 3 trials per category, while standard errors are bracketed.

I : Mean number pre-trial

	S. labiatus			*S. fuscicollis*		
	1	Test	Wilcoxon[1]	1	Test	Wilcoxon
Food	**4.5** (0.3)	**3.2** (0.7)	12.5	**3.0** (0.8)	**2.6** (0.5)	6.5
Non-Food	**4.8** (0.2)	**3.0** (0.8)	10	**2.6** (0.9)	**1.8** (0.2)	12
Wilcoxon (T)	3	2		4.5	12.5	

II : Mean number of BV's

	S. labiatus			*S. fuscicollis*		
	1	Test	Wilcoxon	1	Test	Wilcoxon
Food	**14.5** (0.4)	**8.5** (0.6)	15*	**15.6** (0.9)	**6.7** (0.3)	15*
Non-Food	**7.2** (0.9)	**2.8** (0.3)	15*	**7.0** (0.6)	**2.7** (0.4)	15*
Wilcoxon (T)	15*	15*		15*	15*	

III : Mean latency to approach

	S. labiatus			*S. fuscicollis*		
	1	Test	Wilcoxon	1	Test	Wilcoxon
Food	**4.7** (0.7)	**6.7** (1.1)	14*	**23** (18.9)	**29.3** (11.1)	11
Non-Food	**4.7** (0.9)	**31.5** (15.9)	10	**38.8** (16.5)	**65.5** (33.4)	10
Wilcoxon (T)	10	12		15*	10	

IV : Mean latency to touch

	S. labiatus			*S. fuscicollis*		
	1	Test	Wilcoxon	1	Test	Wilcoxon
Food	**5.6** (0.6)	**7.7** (1.1)	14*	**24.3**(18.8)	**30.4** (11.1)	11
Non-Food	**5.7** (0.9)	**32.5** (15.9)	10	**39.9**(16.5)	**66.4** (33.9)	10
Wilcoxon (T)	10	12		13	10	

V : Mean Time to eat food item

	S. labiatus		*S. fuscicollis*	
	1	Test	1	Test
Food	**8.6** (1.1)	-	**27.7**(19.4)	-
Non-Food	-	-	-	-

Note

[1] Score on Wilcoxon Test , N = 5, between trials.* Significance level set at p=0.05.

Mean latency to approach.

In all categories, the *S. labiatus* approached objects in a quicker mean latency than *S. fuscicollis* (Table 5.AA). There were no significant differences between the two trials for either object category. However, Food objects were generally approached in a quicker mean latency than Non-Food objects, but this difference was only significant for *S. fuscicollis* first trials (T=15, N=5, $p<0.05$).

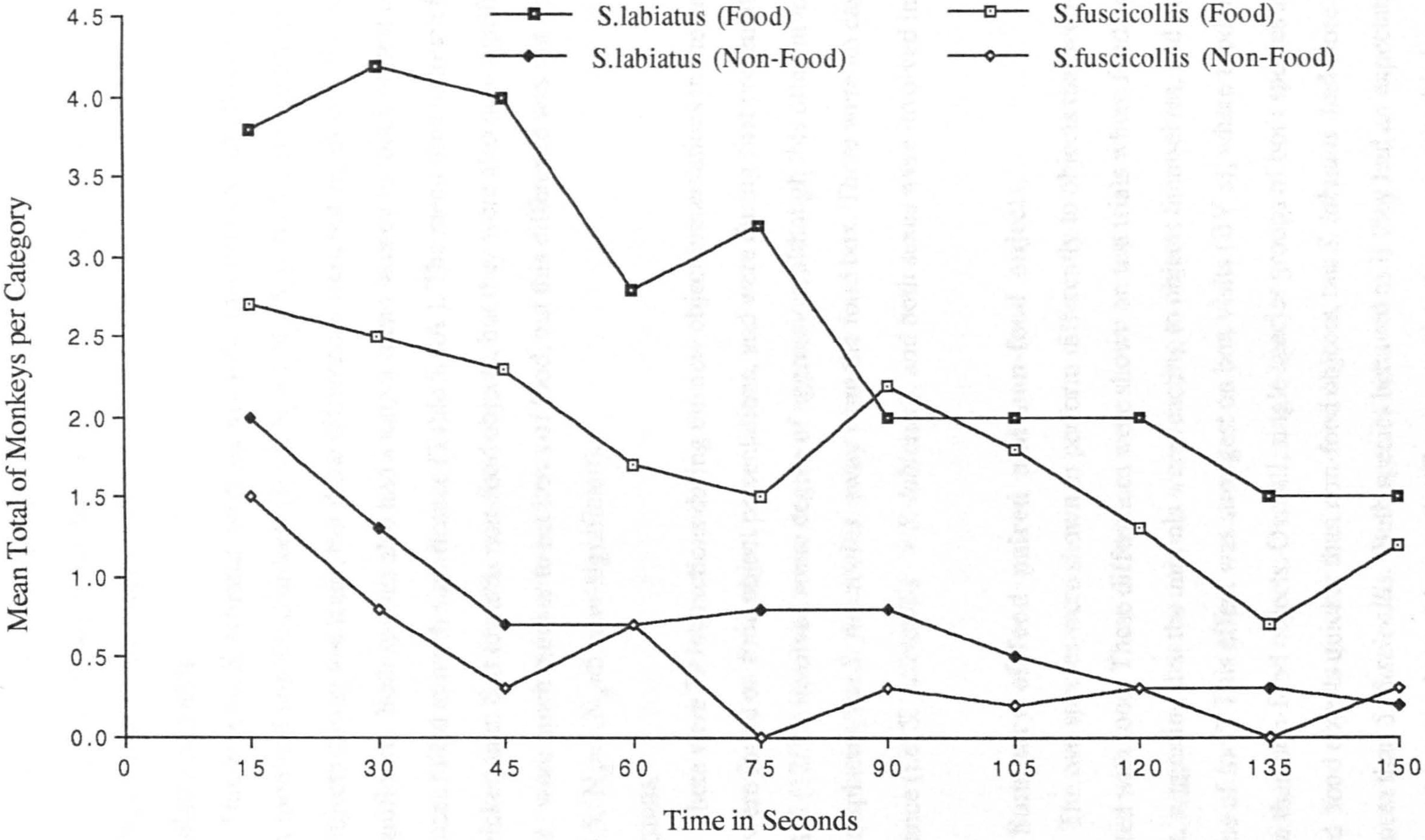


Figure 5.R : Mean number of monkeys present during test trials of novel food and non-food objects

There were no significant differences between the species, in mean latency to approach food objects, during first (U=9.5, N_a=5,N_a=5, non-significant) and test trials (U=6, N_a=5,N_a=5, non-significant). A similar pattern was found for non-food objects, where although *S. labiatus* were first to approach objects on both trials, these differences were not significant (U=11.5, N_a=5,N_a=5, non-significant).

Mean latency to touch.

This time the *S. labiatus* were significantly quicker to touch all objects during first trials of both food and non-food objects (U=3, N_a=5,N_a=5, $p<0.05$). They were also much quicker to touch objects during test trials, but these differences were not significant (U=9, N_a=5,N_a=5, non-significant). Both species also had a longer mean latency to touch on test trials, but these differences failed to reach significance (Table 5.AA). The mean time to touch food objects was also quicker than that towards non-food objects, but they were also non-significant. The *S. labiatus* were much quicker to eat items of food, but this difference was not significant (U=10.5, N_a=5,N_a=5, non-significant).

Interactions.

There were 39 interactions during the new object presentations in the new trials, all of which were found on food object presentations, and were during first presentations only. This time 31% (12/39) involved some degree of aggression, although this often involved a short chase, displacing the *S. fuscicollis* away from the food box. There were no cases of reversal of dominance (i.e. *S. fuscicollis* > *S. labiatus*), and both sexes were involved in interactions.

5.20 Summary of food paired and non-food objects.

The two species were shown to perform differently to objects that were, or were not, presented with food. These differences were shown on test trials where food was not actually present, suggesting that the animals were reacting to objects themselves, and not just to the presence of food. This effect was strongest on box visits (BV's), where food objects had more of these than non-food objects. Overall, single species groups of both species approached and touched food objects quicker than non-food objects, but *S. labiatus* had more significant differences than *S. fuscicollis*. Both species behaved as if they had an expectation of the presence of food in food object trials. They were also shown to retain this learning over a period of at least 17 days. The two species did not significantly differ in their retention response to either food or non-food objects, suggesting that both species were similarly able to retain learning concerned with food availability.

In mixed-species groups, the initial response to objects was related to an expectation of food, where "food" objects had a larger response than "non-food" objects, gained through the single species trials. The *S. labiatus* were generally first to enter the box, but during the divergent trials both *S. labiatus* and *S. fuscicollis* had the greatest number of "initial entries". *S. labiatus* were initially significantly quicker to approach and touch objects that they were trained to regard as "food", but there were no significant differences on objects which were regarded as "non-food". The *S. fuscicollis* reacted more to NF(Sl) / F(Sf) objects and entered the box first, probably because the *S. labiatus* were initially regarding these objects as being "non-food". However, by the test trials the *S. labiatus* were now regarding the NF(Sl) / F(Sf) objects as food, and their dominance allowed them to exploit the initial reaction of *S. fuscicollis.* As *S. labiatus* reacted to F(Sl) / NF(Sf) objects first, because the had been trained to regard them as "food", the subsequent reaction of *S. fuscicollis* on test trials, where they now treated these objects as "food", was probably related to the actions of the *S. labiatus.* This suggests that each species can benefit from the reactions of their congeners.

There was some interaction between the species, but this was mainly concentrated on food objects, which actually contained food items. Typically, the interactions were non-aggressive displacements of *S. fuscicollis* by the more dominant *S. labiatus,* and although a few aggressive chases occurred, there was no serious fighting between the species.

5.21 General discussion of the reaction to food & non-food objects.

In common with other studies of learning in tamarins (e.g. Menzel & Juno, 1982, 1985), it was shown that both *S. labiatus* and *S. fuscicollis* could learn to respond differentially to diverse types of objects after a single trial. This knowledge was at the level of each object either being associated with the presence or absence of of food, and monospecific groups of both species were able to demonstrate a similar level and nature of response. The groups were quicker to approach, touch, and had more box visits (BV's), to objects that had been associated with the presence of food, even during test trials where no food was actually present. This demonstrates that the animals were able to learn to respond to objects due to an expectation of food, and could retain this information for a period of time. The current study had similar results to those produced by previous studies of *S. fuscicollis* (Menzel & Menzel, 1979; Menzel & Juno, 1982, 1984,1985), and suggests that these two species are able to learn about the properties of novel objects after encountering them only once. This learning probably allows tamarins to make the opportunistic use of novel food resources that they may discover in their natural environment, and the retention of such learning for a period in excess of 7 weeks in this study, suggests that both species are able to remember food sources for relatively long periods of time. This ability, allied to a highly developed sense of spatial perception and memory, has been suggested as a major strategy used by tamarins to systematically and efficiently exploit resources within their natural environment (Dolins, 1993; Garber, 1989; Garber & Dolins, 1994; Garber & Hannon, 1993; Garber *et al.*, 1993c).

In mixed-species groups, there is the possibility of a facilitation of this type of learning between the participants (e.g. Buchanan-Smith, 1990a; Pook & Pook, 1982; Terborgh, 1983), and in the current study, such a situation was engineered due to the learning of divergent responses by both species. In this category, one species was trained to regard an object as containing food, while their congeners were trained to regard the same object as not containing food. This allowed an evaluation of the "behavioural facilitation hypothesis", and its relevance to tamarin mixed-species groups. Where *S. fuscicollis* had the appropriate response related to food being present, the main finding was that the initial approach by *S. fuscicollis* during the first presentation of objects in mixed-species trials alerted the *S. labiatus* to the existence of food. On the test trials, the performance of *S. labiatus* was indistinguishable to that shown towards objects that had always been presented with food. On objects where *S. labiatus* had learned about the presence of food, they were usually first to react to such objects. During subsequent trials, the *S. fuscicollis* were now alerted to the presence of food by facilitation of the food related behaviours shown by their congeners, as their performance on these objects was also found to be similar to those given to objects exclusively paired with food. This suggests that both species can gain from the reactions of their congeners, and can use this to their advantage. However, the position is further complicated, due to the fact that the *S. labiatus* had priority of access, and they prevented their congeners from entering the box, until their departure, or until they were satiated and allowed entry to the *S. fuscicollis*. This shows that the *S. labiatus* are likely to be gaining from being in the mixed groups, as they are able to control access to the food items, but for *S. fuscicollis* it is not immediately clear what they gain, as they can be excluded by their congeners. The answer lies in the nature of the food objects, as in every presentation that contained food, there was enough of it present, so that members of both species gained some food items, even though *S. labiatus* were able to gain preferential access to such resources. This pattern clearly has parallells to the position found in wild tamarins in northern Bolivia (Buchanan-Smith, 1989; Chapter 2),where the *S. labiatus* were usually first to enter large feeding trees, and their congeners did not enter until the larger-bodied *S. labiatus* had departed. The case where *S. labiatus* had prior learning about the presence of food, as well as the case where they both had leaned about food, obviously correspond to this pattern, as the *S. labiatus* were first to enter and consume food in these two categories. It supposes that access to these food resources is clearly dependent upon a rigid system of priority , and as the *S. labiatus* are always able to exclude the *S. fuscicollis* from a desired area (e.g. Buchanan-Smith, 1989; Pook & Pook, 1982; Yoneda, 1981,1984b), it follows that they may control access to any previous encountered resources, even though in the present study, monospecific groups of both species have been shown to retain learning about the presence of food equally well. An equivalent pattern has been found in *S. mystax* and *S. fuscicollis* mixed-species groups, where the larger-bodied *S. mystax* are always more dominant, and are first to enter large feeding trees (Peres,1991). Therefore, it is possible that the members of the *S. mystax* group may be able to discover the position of the large non-monopolisable resources found in the middle and upper areas of the forest, and by virtue of their chosen niche (i.e. higher in the forest), and larger body size, are superior to their congeners in the monitoring and exploitation of such resources. Conversely, the *S. fuscicollis*, by the nature of their lower mean height in the forest, are better able to detect and respond to small, monopolisable plant resources, found in the lower area of the forest (Peres, 1991). The position is complicated by the fact that the *S. mystax* are always dominant (e.g. Peres,1991; Chapter 2), and quickly move to displace *S. fuscicollis* from any such small resources. However, as large food sources form the majority of plant feeding in tamarin mixed-species groups (e.g. Buchanan-Smith, 1989; Peres, 1991), and in monospecific groups of *S. fuscicollis*, small feeding trees only contribute a small part of their overall diet (Soini, 1987), then the cost of competition to the *S. fuscicollis*, in terms of loses due to piracy from their congeners, is probably low. For *S. labiatus*, their priority of access over *S. fuscicollis,* means that they have a low degree of direct interspecific competition to contend with, and are also able to gain from the association by exerting their priority in access, where the available amount of food is restricted. This notion is supported by the finding that displacements and aggression between the species were only found where food was actually present. The interactions were mainly displacements, and represent a manifestation of interference competition (Park, 1954), which in combination with exploitative competition (i.e. consuming the food items before others are able), means that the *S. labiatus* have an effective control of the food resources. The fact that they do allow access to *S. fuscicollis*, means that any potential costs due to the presence of these congeners are probably minimal, or at least the costs of defending them are less than any gains the resources may give. This gives a scenario where the costs of behavioural facilitation between the species, concerning food resources, is fairly small, as individuals of both species can gain sufficient food items.

This facilitation of behaviour has been demonstrated to occur in both directions, being facilitated between both species. Arguably, the benefits appear to be asymmetric ; the *S. labiatus* by virtue of its priority of access can monopolise any resources that are limited. This is shown not to be the case, as most resources that are frequently used by both species are superabundant and non-monopolisable, then the *S. fuscicollis* lose little by associating. Also, the behaviour of animals of both species when they encounter food leads to the facilitation of responses to any individual that is close by. Upon detection of food, food related calls have been shown to be delivered by several species of tamarins (e.g.Cleveland & Snowdon, 1982 for *S.oedipus* ; Moody & Menzel, 1976 for *S. fuscicollis* ; Coates & Poole, 1983 for *S. labiatus*), and these may be given when palatable food items are discovered, even when the actual amount found is quite small (Addington *et al.*, 1991). Members of the two species let out specific food calls, when they encountered food, as well as when they initially saw the food related objects on subsequent trials. These calls alerted the members of both species to the presence of food, and may be considered to involve a cost to the individual giving such calls, and this was especially true in the case of *S. fuscicollis* during divergent trials, where they frequently let out such food calls, allowing the more dominant *S. labiatus* to gain from the knowledge of their congeners. This hints that the facilitation of behaviour related to the presence of food may also be gained through auditory signals, and a similar form of reacting to the calls of congeners has been found where both species in tamarin mixed-species groups react to each others alarm calls (e.g. Heymann, 1990c; Peres, 1991). It can be speculated that the facilitation of reactions may be one of the most important benefits an individual accrues from being involved in mixed-species groups, especially if tamarin sociality, as argued by Caine (1994: 201), is based upon "cooperation, tolerance and adaptability " of behaviour. The pattern of within species co-operation is very strong and may involve diverse behaviours such as infant carrying (Price, 1990b; Pryce, 1988), sharing of food items (e.g. Feistner & McGrew, 1989), defending resources (e.g. Garber, 1988a) and in detection of predators (e.g. Bartecki & Heymann, 1987; Moynihan, 1970; Zullo & Caine, 1988). Excluding those behaviours that pertain solely to infant care and breeding success, intraspecific benefits that cooperation and adaptability of behaviour gives to one species, especially in the context of food acquisition, territorial defence and detection of predators, may have the potential to become interspecific benefits through transfer of this information to the associating species. This may only be made possible by the close spatial relationship between the species, that is typically found in mixed-species tamarin groups, and suggests that a high degree of within-species co-operation may have contributed to the evolution of the stable tamarin mixed-species groups.

5.22 Summary of section 5.2.

The two species were also compared in their reactions to the presentation of objects that were presented with or without food. They were shown to respond differentially between food and non-food objects after a single trial. Both species were able to demonstrate a level of response that was comparable with each other, and they could retain this behaviour for a period of at least 7 weeks. In mixed-species groups, there was a tendency for *S. labiatus* to react first to objects, and the priority of access of this species meant that the *S. fuscicollis* had to wait until their congeners had finished, before they gained food items. Nevertheless, they did gain some food items during every trial, and so food objects were non-monopolisable resources. The pattern has parallells with the way the two species exploit medium and large-sized food resources in the wild; the *S. labiatus* lead the progression into such fruit trees, having priority, and the *S. fuscicollis* only enter the tree as their larger-bodied congeners depart. This was the position found where *S. labiatus* had prior learning about the presence of food. In a set of objects where

S. fuscicollis had learned about the presence of food, and *S. labiatus* regarded the object as containing no food, the *S. fuscicollis* were initially first to react, and their congeners only learnt about the food through their reactions. A similar pattern was found for objects which the species had the opposite knowledge. This shows that responses related to the presence of food can be passed between the species, and confirms that the "behavioural facilitation hypothesis" may be a relevant factor in a cost-benefit analysis of tamarin mixed-species groups. This does not mean that both species necessarily benefit to the same degree ; as the potential costs for *S. fuscicollis* may be higher than those for *S. labiatus*, due the priority of access of the latter. However, the costs of feeding competition to both species of tamarins appear to be low, as most food resources exploited by wild tamarins are superabundant and non-monopolisable. Therefore the facilitation of such responses certainly has little cost for *S. labiatus* as they can take any resource they choose to. For *S. fuscicollis*, the costs of losing small resources to their congeners is also fairly low, when compared to the large amount of large food items consumed.

The overall impression is that both species are able to benefit from the facilitation of behaviour between the species, and this probably only has a minimal cost to the species giving the initial response. The two species were also shown to have a differential set of reactions to novel objects, that could be related to both vertical partitioning in the forest, and to foraging techniques shown by tamarins in the wild. These divergent behaviours allow individuals of both species to gain from the responses of their congeners, while forming mixed-species groups.

Chapter 6 : Vigilance and the Reaction of Single Species and Mixed-Species *Saguinus* Groups to the Presence of Threatening Stimuli.

6.0 General introduction.

Predation is a selection pressure which acts upon the lives of primates on an irregular basis, and has been implicated as a strong selective force, shaping the life histories of primates species (e.g. Alexander,1974; Terborgh,1983; van Schaik *et al.*,1983; Stanford, 1989; Struhsaker & Leakey, 1990). Cheney and Wrangham (1987) discuss the notion of predation as being the most important selective pressure leading to primate sociality, but fail to reach any concrete conclusions, due to a paucity in data of actual attacks. They admit, however, that predator-specific alarm calls are suggestive of predation exerting strong selection pressure on at least some aspects of behaviour. Although predation is very rarely observed directly, a review of the reported attacks would appear to indicate that they occur more often in the lives of smaller primates, and that the small South American Callitrichids may suffer the greatest of all (Cheney & Wrangham, 1987). This is emphasised by the findings of Peres (1991), who recorded a rate of one attack by raptors every 8.8 days on his study group of *S. mystax* and *S. fuscicollis.*

6.0.1 Why form mixed-species groups ?

In mixed-species groups, there is an apparent trade-off between the costs and benefits of associating or not associating (see Chapter 1). The advantage of mixed-species troops means that an increase can occur in the number of individuals, without as much feeding competition as would occur with a similarly sized monospecific group. Crucial to the anti-predator hypothesis was the finding of Heymann (1990c), who showed that in a mixed-species group of tamarins both species understood each other's alarm calls, thus giving the opportunity for the facilitation of behaviour related to predation threats.

Heymann (1990b) suggests, that the mere increase in number of potentially vigilant individuals may be sufficiently advantageous for the formation of mixed-species troops in tamarins. Indeed, it has been proposed that this is one way in which mixed-species groups gain from being in association, and has been postulated as a mechanism driving the species to associate; namely the increased anti-predator effects of larger groups without the parallel increase in competition that would occur in similar sized same species groups (Gartlan & Struhsaker, 1972; Gautier-Hion *et. al.*, 1983).

Another way of examining this, is to speculate that one species in an association may "give" the other species a benefit not otherwise attainable to that species (Terborgh & Janson, 1986). This may include ;

(1) Knowledge of locations of ripe fruit within a territory (Gartlan & Struhsaker, 1972; Terborgh,1983; Garber, 1989).

(2) Different responses to novel stimuli or situations (see Chapter 5; Buchanan-Smith, 1989; Garcia, pers. comm.)

(3) Differential responses to predators (e.g. Bartecki & Heymann, 1987; Norconk, 1990b; Peres,1991,1993b).

The idea of species having specialist knowledge about the location of ripe fruit resources within their territory has been shown elsewhere (see Garber, 1989), while differential responses to novelty has been investigated earlier (see Chapter 5). Therefore, the remaining proposal about differential responses to potential predators and /or threatening stimuli will now be investigated.

6.0.2 Reactions to potential predators and threats.

The ability of members of a mixed-species group of tamarins to react differently to different types of threat has been suggested (see Bartecki & Heymann, 1987; Heymann, 1990b) and there is a hypothesis that this is one area of mutual advantage to the associating species. As the *S. fuscicollis* are usually nearer to the ground, they may be more predisposed to react to terrestrial threats more than their congeners, while for the congeners the reverse holds true (see Chapter 1). The congeners are invariably found at a higher average height than *S. fuscicollis* and they may react to potential aerial threats more than the *S. fuscicollis.* This again has been put forward as a mechanism promoting association, but has been largely untested (Buchanan-Smith,1989; Heyman, 1990b; Terborgh,1983). However, recently Peres (1991,1993b) has shown that behavioural differences in mixed-species groups of *S. mystax* and *S. fuscicollis* correspond to height differences, and this can equally apply to both alarm calls and vigilance. In the wild it is often difficult to observe the animals in great detail (Chapter 2), and impossible to control and manipulate conditions carefully. Captive studies can allow researchers to elucidate the key elements of anti-predatory behaviour and to chart changes due to group size and composition.

It is clear from captive studies, that tamarins do monitor their environment, especially if alarming stimuli are presented (e.g. Caine, 1984,1986,1987; Moodie & Chamove, 1990; Price, 1990a). What is unclear, however, is whether or not the surveillance patterns differ for potential aerial and terrestrial predators, and indeed more pertinently for mixed-species groups, how they differ between species. For example, it has been demonstrated that *S. labiatus* monitor their environment by "visual scanning" (Caine 1984, 1986, 1987), but whether or not *S. fuscicollis* use a similar method is not clear. In terms of the dichotomy between aerial and terrestrial threats, there is some indirect evidence from Moody & Menzel (1976), who identified at least 3 different alarm calls given in response to presentation of stuffed owls, unfamiliar humans and to stimuli moved overhead. This suggests sensitivity to different classes of potential predators. Anti-predatory behaviour, as related to group size in tamarins, can give rise to several predictions that are applicable to mixed-species groups of tamarins. In the current study, the main question being addressed is ; Do mixed-species groups offer some degree of improved detection of potential threats when compared to single species groups?

6.0.3 Implications.

Firstly, it may be fair to say that the greater number of tamarins in a mixed-species group, will allow for a better chance of detecting potential predators, than for a group on its own. As mentioned previously, actual predatory events are not observed often, and so we may have to look instead at the levels of active vigilance and their reactions to the presentation of threatening stimuli, when the animals are in and out of association. The main prediction would be that the vigilance rate per unit time would be higher for the mixed group than for each group separately.

6.1 General vigilance in single species captive tamarin groups.

6.1.1 Introduction.

In order to get an accurate description of the forms of vigilance used by both species in an everyday setting, it was necessary to examine the levels of certain categories of behaviours, in an attempt to gain baseline data on general vigilance. While it has been reported that *S. labiatus* monitors its environment by using visual scanning (Caine, 1984), the position is not clearly documented for *S. fuscicollis*. The two species could, however, be examined in terms of the behavioural categories reported in other studies of tamarins, to see if these are appropriate for the current study. These may include such categories as "sit & look" (Vogt *et. al.*, 1978; Vogt, 1978), "look up" (Price,1990a); or also "active scanning" (Caine,1984). As mentioned previously, actual predatory events are not often observed, and so it may be useful to look instead at the levels of active "vigilance", i.e. attending to the environment in a "scanning" sort of way (Caine,1984), and looking-up for aerial predators (Cords,1990a). As *S. labiatus* have been shown to scan their environment (Caine, 1984), this category was considered appropriate, as were several other categories (Table 6.A).

Table 6. A : Selected behavioural definitions of vigilance.

Visual Scanning ; intra- or extra- cage surveillance which was directed at the inanimate environment (i.e. not at cage mates), which was accompanied by sweeping or other visible motions of the head throughout the horizontal plane, and which persisted for at least 10 seconds at any one time (Caine,1984).

Scanning; continuous visual survey of the surroundings as a result of movement of the head or eyes (Hayes & Snowdon,1990).

Look Up; animal looks upwards towards roof or top of enclosure and not at other group members. (Price,1990a).

Visual Fixation ; animals' eyes orientated at a stimuli for at least 1 second [usually used when presenting a threatening stimuli] (Hayes & Snowdon, 1990).

Head Cock ; a distinct rotation of the head [either to left or right] about the longitudinal body axis (Menzel & Menzel, 1980).

6.1.2 Vigilance rate in single species tamarin groups.

Experiment 6.1.A

Do both species display different forms of vigilance, and what are the baseline levels ?

The main purpose of this initial experiment, was to quantify the amount of vigilance shown in each single species group, and to attempt to establish an appropriate behavioural category to describe the vigilance of both species.

6.2 Methods.

6.2.1 Pilot study.

Initially, one group of each species was observed for 2 x 15 minute sample sessions, and the behavioural categories of Table 6.A used to describe vigilance. Initially "visual scanning" (Caine,1984) was omitted, as it was "at least 10 seconds" in duration and therefore not appropriate for instantaneous sampling (Martin & Bateson, 1986). The sessions consisted of instantaneous scan samples of all individuals at 20 second intervals, where all cases of *Scanning, Looking-up, Visual fixation* and *Head-cocking* were noted. It was soon realised however, that visual fixation and head-cocking were not appropriate, as they were stimulus centred and could only be measured when a stimuli was present. The actual definitions were not totally appropriate and so were re-defined as follows :

Look Up : deliberate large single head movement upwards, or stare in an upward direction. Head is usually angled at 45° or more from the horizontal, the head is held static, staring upwards, and not moving from side to side. Animals are not obviously following an insect, nor looking at another animal located above.

Scanning : head is moved from side to side and / or up and down in a continuous flux of movement. Does not include fixated stares and scanning of the floor area, as that usually involves the pursuit of fallen food items, nor does it include scanning during insect foraging.

The exact execution of these behaviours was not exactly identical for the two species. In scanning, for example, *S. labiatus* showed smoother, more deliberate head movements predominantly in the horizontal plane, while *S. fuscicollis* made quicker, sharper and jerkier head movements in all directions. These differences were considered to be mainly qualitative and so each case of scanning was considered to be equivalent. These measures were deemed appropriate to measure baseline vigilance.

6.2.2 Subjects.

Six groups of *S. labiatus* (SL1, SL2, SL3, SL4, SL5 & SL6) and eight groups of *S. fuscicollis* (SF1, SF2, SF3, SF4, SF5, SF6, SF7 & SF8) were tested monospecifically. Each group occupied their own small indoor/outdoor cage system (see Chapter 3 for specific details), and testing was carried out during July & August 1993 and April & May 1994.

6.2.3 General procedure

The amount of vigilance behaviour shown by groups of the two species of tamarins were calculated from 8 x 20 minute sample sessions, conducted in both mornings (0900-1230h) and afternoons (1330-1630h). Sample intervals were set at 20 seconds, and at each point scan samples were taken on all individuals in the group. Only one morning and one afternoon session was conducted for each group on any single day. Each species was tested only on dry days, with the other groups immediately adjacent to the subjects being closed inside, and the subjects themselves were locked into their outside area. Behaviours were recorded on a checksheet (see Appendix 1), where the amounts of looking-up and scanning were noted, as were all occurrences of alarm calling.

6.3 Results.

The data in Table 6.B clearly show that Looking up was the main area of difference between the species, with the *S. labiatus* exhibiting much more of this behaviour than the *S. fuscicollis.*

Table 6.B : Baseline levels of instantaneously sampled vigilance behaviour in two species of captive tamarin monkeys (Totals are means per 20 minute sample sessions).

Saguinus labiatus

Mean per individual[1]

Species	*N*	Look-up	Scanning	All Vigilance	Alarm Calls
SL1	2	6.63	26.44	33.06	0.25
SL2	2	6.13	25.48	31.56	0.75
SL3	2	4.94	27.48	32.38	0.5
SL4	2	5.69	27.06	32.75	0.63
SL5	5	3.20	17.13	20.35	0.65
SL6	2	5.50	27.38	32.81	0.88
Mean		**5.35**	**25.2**	**30.48**	**0.61**
St. errors		**0.49**	**1.60**	**2.10**	**0.09**

Saguinus fuscicollis

Mean per individual

Species	*N*	Look-up	Scanning	All Vigilance	Alarm Calls
SF1	4	1.44	21.25	22.69	0.82
SF2	2	3.5	25.48	28.98	0.32
SF3	2	2.75	27.63	30.38	1.13
SF4	2	2.88	31.5	34.38	0.13
SF5	2	3.06	31.06	34.13	1.5
SF6	2	2.69	25.69	28.38	0.13
SF7	3	2.44	26.38	28.82	0.63
SF8	2	2.25	28.87	31.13	0.5
Mean		**2.63**	**27.23**	**29.86**	**0.65**
St. errors		**0.22**	**1.18**	**1.39**	**0.17**

[1] Rates per individual are extracted from each group individually (i.e. group totals / number of individuals)

The mean amount of looking up per individual was much greater for *S. labiatus* (Mean = 5.35, range 3.2-6.63) than for *S. fuscicollis* (Mean = 2.63, range 1.44 -3.5) and this difference was significant ($U = 1$, $N_a = 6$, $N_b = 8$, $p < 0.01$). The *S. fuscicollis* showed a larger mean amount of scanning (Mean = 27.23, range 21.25 - 31.5) than the *S. labiatus* (Mean = 25.2, range 17.13 - 27.48) and as mentioned previously, these scans were different in execution for

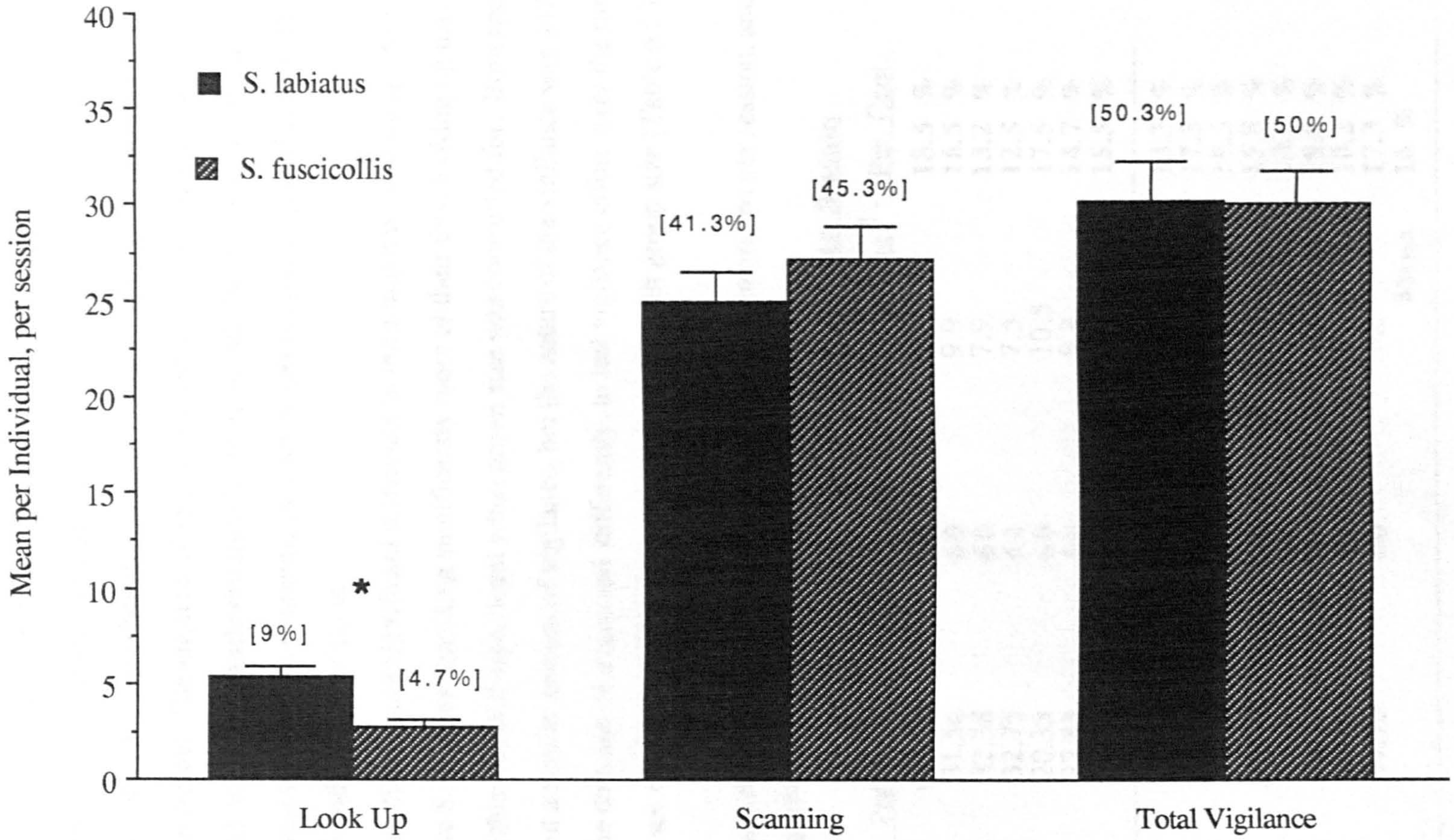


Figure 6.A : Mean vigilance per species, shown as mean scores per individual, per sample session. Bracketed figures Indicate % of occasions in each category.
* = Significance on Mann-Whitney, $p< 0.01$.

each species. However, unlike the the looking up data, the difference was non-significant (U =17.5, N_a =6, N_b =8, non-significant; Figure 6.A). This shows that the two species do not differ in their amount of scanning. The amount of overall vigilance was very similar and was not significantly different, even though *S. labiatus* had a larger mean amount (U =18, N_a =6, N_b =8, non-significant). The mean number of alarm calls per individual for each species was very similar, and not significantly different (U =22, N_a =6, N_b =8, non-significant). This suggests that there is no reason to assume that either species was subjected to more threatening stimuli during baseline observations.

However, there was a significant difference in the amount of looking up shown by each species, with the *S. labiatus* spending significantly more of their time looking up than the *S. fuscicollis*, and this was still significant when group size was controlled for. Both species in effect carried out a similar amount of vigilance, but the nature of the vigilance was different. Furthermore, the data can be examined differently, to test vigilance effort over the sample session, and to see exactly how vigilant behaviour varies with group size (Table 6.C).

Table 6.C : Mean rate of vigilance shown by captive tamarin groups per session, and the level of zero vigilance.

		Vigilance Measures Per Session			
Group	N	Per Individual	Total Possible[1]	Zero Vigilance[2].	Per Cent.
SL1	2	33.06	60	11.1	18.5 %
SL2	2	31.56	60	9.9	16.5 %
SL3	2	32.38	60	7.9	13.2 %
SL4	2	32.75	60	7.5	12.5 %
SL5	5	20.33	60	10.5	17.5 %
SL6	2	32.81	60	8.8	14.7 %
				Mean	15.5 %
SF1	4	22.69	60	8	13.3 %
SF2	2	28.98	60	10.4	17.3 %
SF3	2	30.38	60	11.6	19.3 %
SF4	2	34.38	60	9.5	15.8 %
SF5	5	34.13	60	8.9	14.8 %
SF6	2	28.38	60	11.9	19.8 %
SF7	3	28.82	60	6.1	10.2 %
SF8	2	31.13	60	10.7	17.3 %
				Mean	16 %

[1] This maximum assumes that at any single point in time, there is one or more individual engaged in vigilance, in effect a sentinel or "guard" role.

[2] Zero vigilance is the mean number of sample intervals where no individuals were being vigilant.

All groups show some vigilance for most of the time, as every group had at least one individual vigilant for over 80% of the sample points. As a result, there is usually at least one animal being vigilant at any single point at time, and vigilance is therefore a very important part of the tamarins' behavioural repertoire. There was no simple relationship between vigilance and group size, especially in *S. labiatus* where the largest group had the second highest mean amount of zero vigilance. For *S. fuscicollis* , the two larger groups had the lowest amount of zero vigilance, but the largest group did not have the lowest amount of zero vigilance. The rates per individual were different for larger groups when compared to pairs, where each individual in the group has to be vigilant for relatively less occasions than in the case for simple pairs. As individuals were not identified, one important factor in accounting for these differences may be variations in vigilance rates of some particular individuals. One way of examining this was to compare the amount of vigilance units per group (where 1 unit = 1 subject engaged in vigilance per sample point) .

Table 6. D : Total vigilance effort for two species of tamarins, during monospecific baseline trials.

Saguinus labiatus

Species	*N*	**Mean Vigilance**	**Group Vigilance**
SL1	2	33.06	66.12
SL2	2	31.56	63
SL3	2	32.38	64.76
SL4	2	32.75	65.5
SL5	5	20.33	101.65
SL6	2	32.81	65.62

Saguinus fuscicollis

Species	*N*	**Mean Vigilance**	**Group Vigilance**
SF1	4	22.69	90.76
SF2	2	28.98	57.96
SF3	2	30.38	60.76
SF4	2	34.38	68.76
SF5	2	34.13	68.26
SF6	2	28.38	56.76
SF7	3	28.82	86.46
SF8	2	31.13	62.26

Nevertheless, Table 6.D shows that there were more total vigilance units in the two largest groups (mean vigilance per ind. X number of ind.). Also that in the larger groups each member had relatively less vigilance to perform over the period, while the group as a whole had more vigilance units when compared to pairs. This was the case for both species. However, group SF7 with 3 group members also had an increased amount of vigilance units, but did not have a similar reduction in the mean amount of vigilance per individual. The largest groups of both species each had a pair of juvenile offspring in them, and it remains possible that they did not contribute as much to vigilance as the adults, giving a reduction in the mean rate per individual.

6.4 Conclusions.

Looking up and scanning both occurred at high frequencies for both species, and at most points in time there was usually one or more individuals engaged in some form of vigilance. This is suggestive of a "guard" role. The nature of this vigilance varied between the species and the *S. labiatus* showed significantly more looking up, but not any more total vigilance than *S. fuscicollis.* The larger groups have more total vigilance, but may also generally less vigilance per individual, than had smaller groups.

6.5 Mixed group general vigilance

It was clear that monospecific groups of both species monitor their environment, and that the 2 species differ only in terms of looking up. Their behaviour is now compared when they are participants in mixed-species groups.

Experiment 6.1.B

Do mixed-species groups give anti-predatory advantages for the individuals participating in them ?

6.5.1 Introduction.

Firstly, it may be justified to say that the greater number of tamarins in a mixed-species group, allow for a better chance of detecting potential predators, than for a group on its own. This would be achieved through an increase in numbers, giving an increase in the number of eyes and ears that could passively detect potential threats, as well as any advantages due to the active monitoring for predators (see Chapter 1, Section 1.1).This may suggest that they are better able, or at least more likely, to encounter aerial threats than their congeners.

What may occur in mixed-species groups, will depend on how the two species organise their vigilance. The position would basically involve 2 separate hypotheses : 1) Both species independently adjust their vigilance patterns only according to their own species, and will show no change in their vigilance when in mixed groups, or 2) One or both of the species will adjust their rate of vigilance, due to the association, and the level of vigilance will differ to that shown when in monospecific groups. This comparison forms the basis for experiment 6.1A.

It is probable, that no matter whichever of these hypotheses is supported, there will be two predicted outcomes. Firstly, as long as neither species reduces their vigilance by a large degree, then the vigilance rate per unit time will be higher for the mixed group than for each group separately. Secondly, individuals in groups of *S. fuscicollis,* when in mixed-species groups, may benefit from the larger proportion of looking-up shown by *S. labiatus*. A similar pattern has been demonstrated for *S. mystax -S. fuscicollis* associations, where the *S. mystax*, which have a higher mean height in the forest than their congeners, and are found to be more vigilant for aerial predators (Peres, 1991,1993d). This suggests that in the current study, the *S. fuscicollis* may benefit from a similar monitoring of aerial predation threats when in mixed groups.

These predictions will hold true, especially if the the two species tend to exhibit vigilance patterns that are dependent solely upon the number of their own species, regardless of their congeners. However, as long as any decrease in vigilance is not too large for either species, these predictions will still be met. The two species are compared below.

6.6 Methods.

6.6.1 Subjects.

Mixed groups were formed from five pairs of each species (GP3 : SL1 & SF3; GP4 : SL2 & SF5; GP6 : SL4 & SF8; GP7 : SL3 & SF6; GP8 : SL6 & SF2). Each mixed species group was housed in a separated double indoor / outdoor cage system, and all mixed groups were separated from each other by at least one adjacent cage, containing a different species of callitrichids (see Chapter 3 for details). Testing was carried out between July and August 1994.

6.6.2 General procedure.

The procedure was identical to that of Experiment 6.1.A, except that both species within the mixed species-groups were sampled concurrently. All other adjacent groups of monkeys were closed into their indoor areas, to minimise distractions to the study groups. For the duration of the sample session, the mixed group being studied was locked outside, in only one of their own areas to facilitate scan sampling. In order to standardise observation conditions, vigilance was once again calculated from 8 x 20 minute sample sessions, conducted in both mornings (0900-1230h) and afternoons (1330-1630h), and at each point scan samples were taken on all individuals in the group. Only one morning and one afternoon session were conducted for each group on any single day, and once again behaviours were recorded on a checksheet, as were all occurrences of alarm calling.

6.7 Results.

6.7.1 Single species vigilance.

In order to chart the changes that occurred due to vigilance in mixed species groups, it was first necessary to compare the vigilance in the five groups of each species that were selected to be mixed. Table 6.E shows that these selected groups followed the species' pattern, with the only significant difference being that the *S. labiatus* looked up more than the *S. fuscicollis* did ($U=0$, $N_a=5$, $N_b=5$, $p<0.01$). Overall, the *S. labiatus* had a higher mean amount of vigilance (32.3 per individual, per session) than their congeners (30.6), but once again this did not reach significance ($U=5$, $N_a=5$, $N_b=5$, non-significant). *S. fuscicollis* had a marginally higher mean amount of scanning, but once again this difference was not large enough to be significant ($U=8.5$, $N_a=5$, $N_b=5$, non-significant). Both species also spent over 80% of the sample points being engaged in vigilance, and this was not significantly different ($U=6$, $N_a=5$, $N_b=5$, non-significant).

Table 6.E : Level of instantaneously sampled vigilance in 5 single species groups of *Saguinus labiatus* and *S. fuscicollis*, before formation of mixed-species groups (Totals are means per 20 minute sample sessions ; * = Significance on Mann-Whitney, $p< 0.01$, ns = Non-significant).

		S. labiatus					*S. fuscicollis*		
		Mean Per Individual[1]					Mean Per Individual[1]		
Species	*N*	Look-up	Scan	All Vigilance	*Species*	*N*	Look-up	Scan	All Vigilance
SL1	2	6.6	26.4	33.1	SF2	2	3.5	25.5	29.0
SL2	2	6.1	25.5	31.6	SF3	2	2.8	27.6	30.4
SL3	2	4.9	27.5	32.4	SF5	2	3.1	31.1	34.2
SL4	2	5.7	27.1	32.8	SF6	2	2.7	25.7	28.4
SL6	2	5.5	27.4	32.9	SF8	2	2.3	28.9	31.2
Mean		5.8^{*}	26.8^{ns}	32.6^{ns}			2.9^{*}	27.7^{ns}	30.6^{ns}
St. errors		0.29	0.33	0.35			0.21	1.04	1.00

[1] Rates per individual are extracted from each group individually (i.e. group totals / number of individuals)

6.7.2 Mixed-species vigilance.

When examined in mixed-species groups (Figure 6.B), the two species showed a near identical patterning of vigilance to the single species condition, in terms of where the differences were found (Table 6.F). The only significant difference was that the *S. labiatus* once again looked up more than their congeners, ($U=0$, $N_a=5$, $N_b=5$, $p<0.01$). Both scanning and total vigilance patterns were similar to before, and were not significantly different ($U=9$, $U=7$, $N_a=5$, $N_b=5$, non-significant). The groups of both species also spent an equivalent and non-significant amount of time engaged in vigilance, both averaging around 79% of observations ($U=12$, $N_a=5$, $N_b=5$, non-significant). Therefore, it was apparent that groups of both species were behaving similarly, with respect to each other, in both conditions.

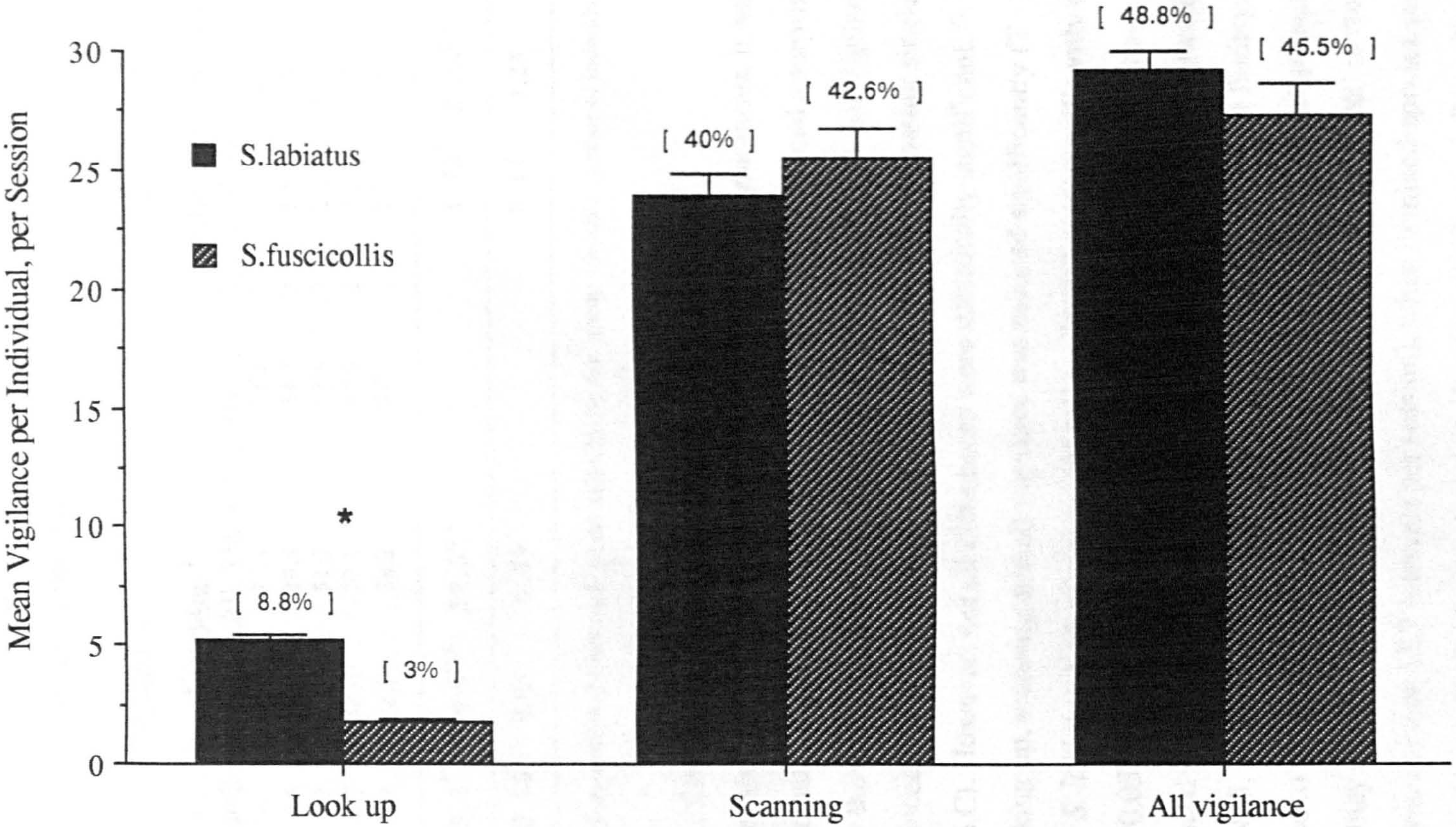


Figure 6.B : Mean vigilance per species, during mixed-species groups, shown as mean scores per individual, per sample session. Bracketed figures indicate % of occasions in each category. * = Significance on Mann-Whitney, $p < 0.01$.

Table 6.F : Level of Instantaneously Sampled Vigilance Behaviour in Five Captive Mixed-Species Groups of *Saguinus labiatus* and *S. fuscicollis*. (Totals are means per 20 minute sample sessions ; * = Significance on Mann-Whitney, $p < 0.01$, ns = Non-significant).

		S. labiatus					*S. fuscicollis*		
		Mean Per Individual[1]					Mean Per Individual[1]		
Species	*N*	Look-up	Scan	All Vigilance	*Species*	*N*	Look-up	Scan	All Vigilance
SL1	2	5.3	22.1	27.4	SF2	2	1.8	24.2	26.0
SL2	2	5.4	24.4	29.8	SF3	2	1.6	26.9	28.5
SL3	2	4.7	27.0	31.7	SF5	2	2.2	29.1	31.3
SL4	2	5.7	23.6	29.3	SF6	2	1.7	21.7	23.3
SL6	2	5.3	22.9	28.2	SF8	2	1.7	25.8	27.5
Mean		5.3^{*}	24.0^{ns}	29.3^{ns}			1.78^{*}	25.5^{ns}	27.3^{ns}
St. errors		0.16	0.85	0.79			0.11	1.25	1.31

[1] Rates per individual are extracted from each group individually (i.e. group totals / number of individuals)

6.7.3 Single vs. mixed group vigilance per species.

As species specific differences were maintained in the two conditions, it was appropriate to compare the actual numerical differences within species. This produced a surprising result (Table 6.G). For the active vigilance categories (Look Up, Scanning & All Vigilance) there was a pattern of a reduced amount of vigilance for both species, when comparing single and mixed groups (Figure 6.C). However, not all differences were statistically significant. For *S. fuscicollis,* looking up, scanning and all vigilance was reduced significantly (T=15, N=5, $p < 0.05$), while in *S. labiatus* both scanning and "all vigilance" were significantly different (T=15, N=5, $p < 0.05$), but not looking up. Table 6.G also shows that the amount of alarm calling was reduced in the mixed species presentations, but this was not significant for either species (T=10, N=5, non-significant), so probably did not account for the findings.

Compared to single species trials, *S. labiatus* had a significantly larger number of occasions when they engaged in "zero" vigilance (i.e no individuals engaged in recognised vigilance behaviours : mean 12.7 intervals per session), when in mixed-species groups (T=15, N=5, $p < 0.05$). Although *S. fuscicollis* had a similar amount of zero vigilance to *S. labiatus,* when in mixed groups (mean 12.9), this was not significantly greater than that shown in single species groups (T=12, N=5, non-significant).

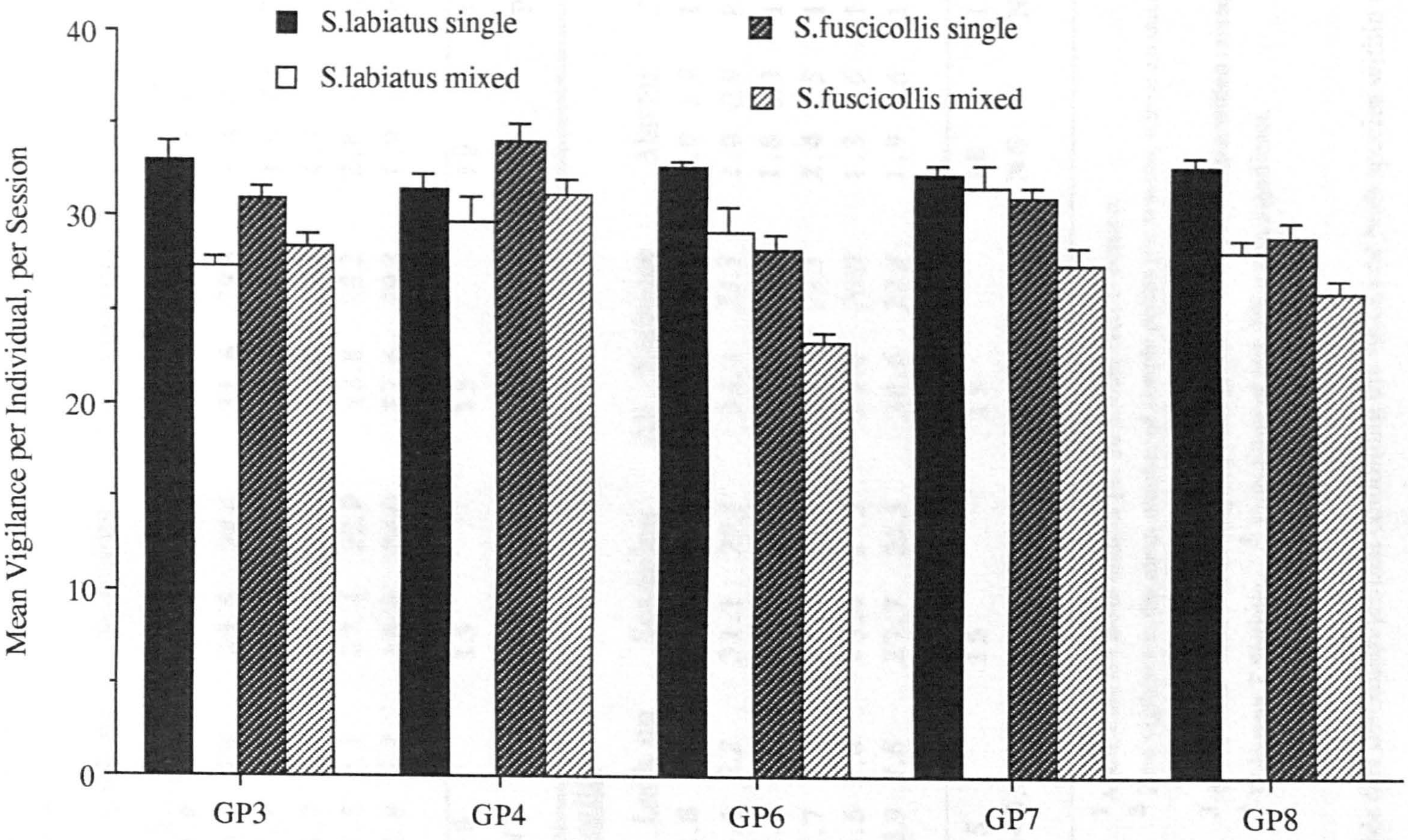


Figure 6.C : Mean vigilance per individual, per session, for both single and mixed-species groups of tamarins.

Table 6.G : Comparison of vigilance shown by members of five mixed-species groups, when tested in both single and mixed groups. Scores for vigilance are reported as mean score per session, per individual.

S. labiatus

	Look up		Scanning		All Vigilance		Alarms[1]		"Zero"[2]	
Group[3]	S	*M*	S	*M*	S	*M*	S	*M*	S	*M*
SL1	6.6	*5.3*	26.4	*22.1*	33.1	*27.4*	2.3	*1.9*	11.1	*14.1*
SL2	6.1	*5.4*	25.5	*24.4*	31.6	*29.8*	1.4	*0.9*	9.9	*10.7*
SL3	4.9	*4.7*	27.5	*27.0*	32.4	*31.7*	1.0	*2.3*	7.9	*11.0*
SL4	5.7	*5.7*	27.1	*23.6*	32.8	*29.3*	1.9	*1.5*	7.5	*12.8*
SL6	5.5	*5.3*	27.4	*22.9*	32.8	*28.2*	2.8	*1.6*	8.8	*14.1*
Mean	5.8	*5.3*	26.8	*24.0*	32.6	*29.3*	1.9	*1.6*	9.4	*12.7*
T[4]	10		15		15		10		15	
Sig.[5]	NS		p<0.05		p<0.05		NS		p<0.05	

S. fuscicollis

	Look up		Scanning		All Vigilance		Alarms		"Zero"	
SF3	2.8	*1.6*	27.6	*26.9*	30.4	*28.5*	2.0	*1.9*	11.6	*10.8*
SF5	3.1	*2.2*	31.1	*29.1*	34.1	*31.3*	2.0	*0.9*	8.9	*8.4*
SF8	2.3	*1.7*	28.9	*25.8*	31.1	*27.5*	1.8	*2.3*	10.7	*13.9*
SF6	2.7	*1.7*	25.7	*21.7*	28.4	*23.3*	2.4	*1.5*	11.9	*17.8*
SF2	3.5	*1.8*	25.5	*24.2*	29.0	*26.0*	1.3	*1.6*	10.4	*13.9*
Mean	2.9	*1.8*	27.7	*25.5*	30.6	*27.3*	1.9	*1.6*	10.6	*12.9*
T	15		15		15		10		12	
Sig	p<0.01		p<0.05		p<0.05		NS		NS	

[1] Alarm calls are mean number per 20 minute sample session.

[2] Zero vigilance is the mean number of sample points per session, where no members of the group were engaged in vigilance.

[3] S = Scores when within single species groups M = Scores when within mixed species groups

[4] Wilcoxon T Statistic. [5] Probability of test, NS = non-significant.

Table 6.H demonstrates that combining the results of both species within mixed groups, the mean amount of vigilance per mixed group, averages over 100 units of vigilance (1 unit = 1 subject engaged in vigilance per sample point). This exceeds any mean value found in the single species conditions (Table 6.D), even though one group of *S. labiatus* had 5 members (mean 96.8 units) and one group of *S. fuscicollis* had 4 members (mean 90.76 units). The paucity of

data allows little scope for comparison, but the tentative finding is that all mixed groups had a larger mean amount of vigilance units than the large single species groups.

Table 6.H : Total vigilance effort for two species of tamarins during mixed-species trials.

Group		*N*	Mean [Group mean]		Group Effort
GP3	SL1	2	27.4	[27.9]	111.7
	SF3	2	28.5	[27.9]	
GP4	SL2	2	29.8	[30.5]	122
	SF5	2	31.3	[30.5]	
GP6	SL4	2	29.3	[26.3]	105.2
	SF6	2	23.3	[26.3]	
GP7	SL3	2	31.7	[29.6]	118.4
	SF8	2	27.5	[29.6]	
GP8	SL6	2	28.2	[27.6]	110.4
	SF2	2	26.0	[27.6]	

Another advantage found in mixed-species groups, where the species tend to behave fairly independent of each other (see Chapter 4), is that the amount of time when there are no individuals being vigilant is reduced, when compared to the groups of each species individually. Specifically, the number of sample points in which a mixed-species group as a whole exhibits no vigilance, is less than that shown by each of the two species on their own. Figure 6.D shows that all mixed groups had a combined score of only 3.8 - 6.3% of time not engaged in vigilance, but single species groups of *S. labiatus* and *S. fuscicollis* had respectively 12.5 - 18.5% and 14.8 - 19.8% of time not carrying out vigilance. This means that both species benefit from more vigilance per unit time, when in mixed groups, and this was significantly larger for both *S. labiatus* ($U=0$, $N_a=5$, $N_b=5$, $p<0.01$) and *S. fuscicollis* ($U=0$, $N_a=5$, $N_b=5$, $p<0.01$). However, within these mixed groups, both species tended to have an increased amount of individual "zero" vigilance, compared to single species sessions. Even though *S. fuscicollis* had a substantial reduction, this was not a significant decrease ($T=12$, $N=5$, non-significant), while in *S. labiatus* this pattern was clearly significant ($T=15$, $N=5$, $p<0.05$). So both species in the mixed groups spent a reduced amount of time engaged in vigilance, but gained from the vigilance of their congeners, leading to a larger number of vigilance units.

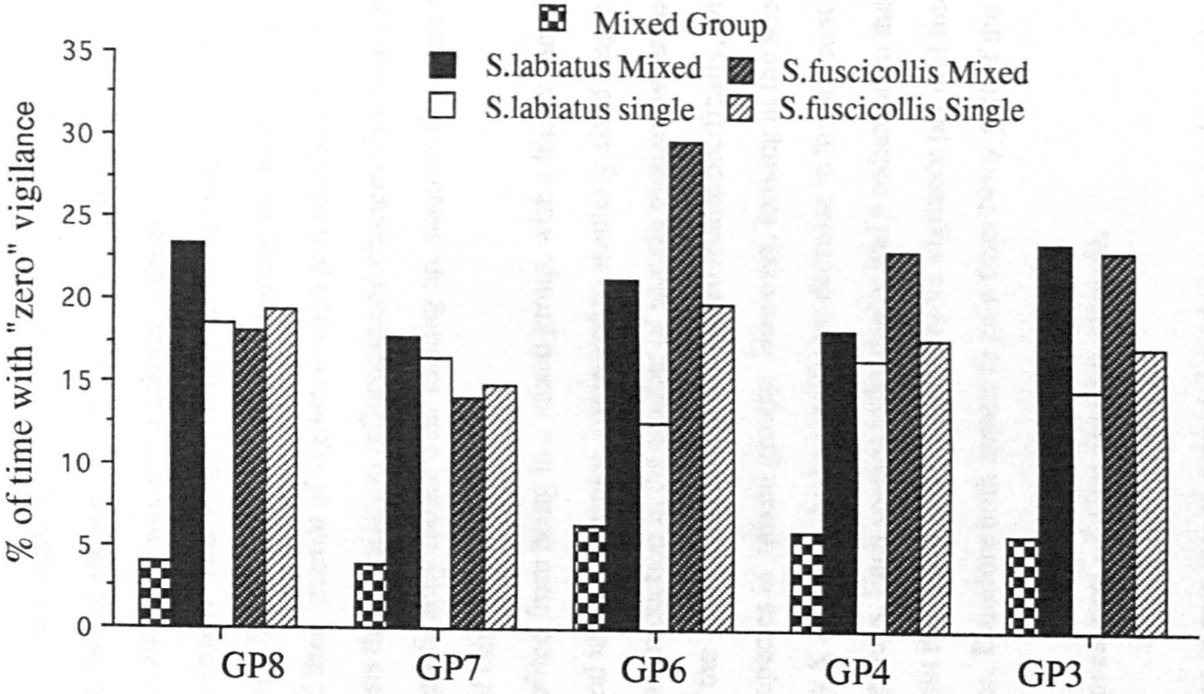


Figure 6.D : Level of "zero" vigilance shown by 5 groups of two species of tamarins, when combined in mixed groups, separate within mixed groups and in single species Groups.

6.8 Summary.

The five groups of *S. labiatus* sampled monospecifically, showed no significant difference in the amount of total vigilance when compared to monospecific groups of *S. fuscicollis*, although the former showed significantly more looking up. This pattern was repeated in mixed groups, and there was also a general decrease in all categories of vigilance in the mixed groups. *S. fuscicollis* had a significantly decreased amount in all categories, while *S. labiatus* only had a significant reduction in both scanning and total vigilance. This suggests that both species adjusted their amount of vigilance when part of mixed-species groups, giving evidence for the hypothesis that association influences and changes vigilance patterns. The fact that *S. labiatus* did not significantly reduce their looking up, suggests that there may be a species-specific pattern of this type of vigilance.

Both species benefited from being in a mixed group, with a higher mean amount of vigilance units being found in mixed groups, compared to similarly sized single species groups. There was also a significant reduction in the number of sample sessions where no individuals were vigilant, comparing the groups of each species tested monospecifically, with the combined scores of both species in mixed groups. However, looking at the scores of each species on their own, only *S. labiatus* had a significant decrease in the amount of zero vigilance when in mixed groups. Each species individually had a reduction in the amount of vigilance they exhibited, but the group as a whole had more vigilance per unit time and a smaller amount of "zero" vigilance. Therefore both appear to gain from being part of the mixed group.

6.9 Reaction to the presence of threatening stimuli.

Experiment 6.2

How does vigilance change in response to potential predators and or threatening stimuli?

6.9.1 Introduction.

How the species respond to the presence of threatening stimuli monospecifically, could potentially be an area of divergence between the species. The main purpose of this study was to examine the reaction of the species to threatening stimuli. In this set of experiments the reactions of the species were compared monospecifically, in their reaction towards the presentation of "threatening stimuli". Threatening stimuli are operationally defined as stimuli that incite alarm and / or fear in the monkeys immediately upon their presence being discovered. These items elicit a very different response to those that were presented as "novel objects" (see Chapter 5).

The theoretical consideration being that the stimuli should incite fear in the monkeys (presumably due to novelty and potentially threatening nature of the stimulus) but should eventually become approachable. This allowed me to compare the reactions of the two species and to draw some conclusions as to similarities and differences in "dealing with mild threats" shown by the animals. The present study attempted to test whether the 2 species behave differently to threatening stimuli and/or potential predation threats. In addition, it allows me to test, at least partially, the theory that each species may be individually more predisposed to detect, alert others, or even "deal with" different classes of predators.

6.10 Methods.

6.10.1 Subjects.

Four groups of *S. labiatus* (SL2, SL3, SL4 & SL5) and four groups of *S. fuscicollis* (SF1, SF2, SF4 & SF5) were tested in this study. All were housed in the same indoor / outdoor areas as before (For details see Chapter 3).

6.10.2 Stimuli.

Initially, it was necessary to discover which stimuli the animals regarded as threatening. Stimuli were selected on the basis of the tamarins' initial response upon presentation. Following the work of Caine (1986), the procedure involved the placing of a stimulus thought to be threatening, in front of the cage for 30 seconds, and if piloerection and alarm calls are shown, the stimulus was defined as threatening. The stimuli eventually chosen as threatening, were those which at least two groups of each species reacted to, and to which four or more separate alarm calls were given. This was not very easy to fulfil, as many stimuli that were initially selected to be used, failed to meet even this criterion.

Quickly it became apparent that although they initially caused some fear, "stuffed" animals were not very frightening, and therefore some live animals were used. This was in line with the findings of Hayes & Snowdon (1990), who determined that movement in live animals was considered to be a major fear inducing stimulus, and also those of Bayart & Anthouard (1992) who found that snakes often caused fear in primates. The chosen stimuli were sub-divided into 2 classes of threat ; very threatening (VT), a fearful reaction was shown and many alarms (8 or more alarm calls) are shown by all groups, and mildly threatening (MT), where only the lowest definition (i.e. four alarm calls) of 'threatening' was reached by at least 2 of the groups. The two conditions are separated by the number of alarm calls, all MT objects had < 8 alarm calls shown by all groups, while VT objects elicited more than 8 alarm calls from all groups. The VT stimuli all had the largest percentage of time spent in movement, with all stimuli moving for more than 30% of the sample session, and this was considered to be pertinent in the level of alarm they caused. Eventually, three threatening stimuli were selected for each category, and 3 control presentations were also conducted. All the stimuli selected are shown in Table 6.I.

Table 6.I : Stimuli used during threatening stimuli trials.

Control stimuli :	1) **No stimuli**, apparatus only. 2) **Wooden Log** , 15cm long, 10cm diameter. 3) **Cardboard Box**, 20 x 12 x 12 cm.
Mild Threatening (MT):	1) **Barking Toy Dog**, brown and furry, moved when intermittently barking, approximately 5-10% of time. 2) **Live Rabbit** (*Oryctolagus cuniculus*) did not move during trials. 3) **Stuffed Stoat**, in standing pose.
Very Threatening (VT):	1) **Florida King Snake**,(*Lampropeltis getalus floridana*) moved around for approximately 25% of the time. 2) **Bull Frog**, (*Rana catesbiana*) jumped around for more than 40% of the time. 3) **Yellow Rat snake** (*Elaphe guttata quadrivittata*) moved around for around 30% of the time.

6.10.3 Procedure.

The order of presentation to each species of stimuli was randomised, and each species was tested in visual isolation from each other. The time of sample session was divided between morning and afternoon to counterbalance time of day effects. In total, 9 x 15 minute trials were conducted for each species. Sampling methodology was split between instantaneous scan samples (20 second sample interval), all occurrence samples, and the duration to initial approach. The following behavioural data was sampled ;

Initial Occurrences ;

(i) Alarm calls ; where they occurred, these were sampled only to re-confirm a stimulus was threatening. Alarms obviously directed towards something other than the stimulus (e.g. a bird flying overhead) were not included.

(ii) Each attempt to approach (< 75 cm) the stimulus was noted, where only distinctive approaches (including full withdrawals) were noted. This was recorded because during a pilot study, the *S. fuscicollis* tended to make frequent approaches and withdrawals towards stimuli, and this distance adequately represented such approaches.

Actual Duration ;

(iii) The duration for the first individual to approach to within ; a) 1 m, b) < 50 cm, c) < 15 cm, and d) to touch

At Scan Samples :

(iv) The distance of each monkey from the stimuli was noted at three distances ; a) 0 cm b) < 15cm c) 15-50cm

(v) Measures of vigilance ; for each species, scanning and looking up was recorded as before, in addition visual fixation on the stimuli was recorded (definition as in Table 6.A).

6.10.4 Test protocol.

The tests were carried out as follows;

1) The stimulus to be tested was selected, and the group to be tested was shut into their indoor area. Adjacent groups were also locked into their inside areas.

2) The selected stimulus was placed inside a plastic tank, 40 x 30 x 30 cm, which had air holes in the lid. The tank was placed on top of a 25 cm high metal stand, placed in the outside area and was subsequently hidden by a cover. The cover was attached by a cord to a hole in the roof, from where it could be removed from on top of the tank.

3) The animals were allowed out and were subsequently shut outside. The sample session began when the cover was removed.

4) The behaviours were sampled over a 15 minute sample period, and durations were measured using a stopwatch. Sample intervals were timed by means of a metronome. Once the session was completed, the stimulus was removed and all animals were allowed free access inside and outside.

All sample sessions were carried out on similar days (i.e. dry mild days), and each category of stimulus was varied, so that adjacent sample sessions did not use the same type of stimulus. Every session was conducted on a different day, so that they could be considered independent of each other. Due to small sample numbers, non-parametric statistical methods were appropriate. Mann-Whitney U-tests were used to test differences between the species, Wilcoxon Signed Ranks tests were used to determine with species differences between conditions, while Pages-L test was used to test if the degree of response was related to the threat of stimulus (Siegel & Castellan, 1988). Significance was set at $p = 0.05$, two-tailed for approaches and duration to approach, as direction of effect was unclear. For vigilance, a one-tailed test was appropriate as it was predicted to increase with degree of threat.

6.11 Results.

6.11.1 Alarm calls.

These were noted during the experiment, only as an indication that the nature of the chosen stimuli (which had already been assigned to the appropriate category) had not changed since their initial assignment, and it is therefore not appropriate to analyse them statistically. In Table 6.J, it is clear that not one of the control stimuli elicited enough alarm calls to be considered 'threatening', and this confirms their status as controls. This does not indicate that absolutely no alarm was shown upon removal of the cover, but this was typically restricted to one, or occasionally two alarm calls, and was different to the other 'threatening' stimuli. The very threatening (VT) stimuli all easily reached the threatening criterion (of 8 alarm calls), and this emphasises their stronger threat and / or having a more dangerous element. Not all of the mild threat (MT) category reached the "mildly threatening" level (4 alarm calls), but all had at least 2 groups responding to them with the appropriate level of alarm shown towards them. The overall categorisation of stimuli were therefore appropriate, and could be used in analysis.

Table 6.J : Alarm calls shown upon presentation of stimuli during threatening stimuli trials (Yes indicates that at least the minimum number of alarm calls were shown towards the stimuli ; 4 calls for mild threats, and 8 alarm calls for very threatening objects).

	Control stimuli			Mild Threat			Very Threatening		
	1	2	3	1	2	3	1	2	3
SF1	X	X	X	Yes	Yes	X	Yes	Yes	Yes
SF2	X	X	X	Yes	X	Yes	Yes	Yes	Yes
SF4	X	X	X	Yes	Yes	Yes	Yes	Yes	Yes
SF5	X	X	X	Yes	Yes	Yes	Yes	Yes	Yes
SL2	X	X	X	Yes	Yes	Yes	Yes	Yes	Yes
SL3	X	X	X	Yes	Yes	X	Yes	Yes	Yes
SL4	X	X	X	X	X	Yes	Yes	Yes	Yes
SL5	X	X	X	Yes	X	Yes	Yes	Yes	Yes

6.11.2 Vigilance shown to stimuli.

As all groups were not similarly sized, it was appropriate to examine the amount of vigilance on a 'per individual' basis. The vigilance shown towards the stimulus included *Visual Fixation* (see Table 6.A), as this was directed unequivocally towards the stimulus, and could now be noted. The results were initially compared between the species, to see if the species behaved similarly.

The results clearly show that there were no significant differences between the level of vigilance shown by both species, in any of the conditions individually or in the overall results (Table 6.K). In all cases, the *S. fuscicollis* showed slightly more vigilance. For all groups of both species, the amount of vigilance increased over the three conditions, and corresponded to the alarm evoking power of the stimulus (Figure 6.E). The pattern of an increased amount of vigilance for increased threat was found for both species (Pages $L_{(3,4)} = 56$, $p<0.01$).

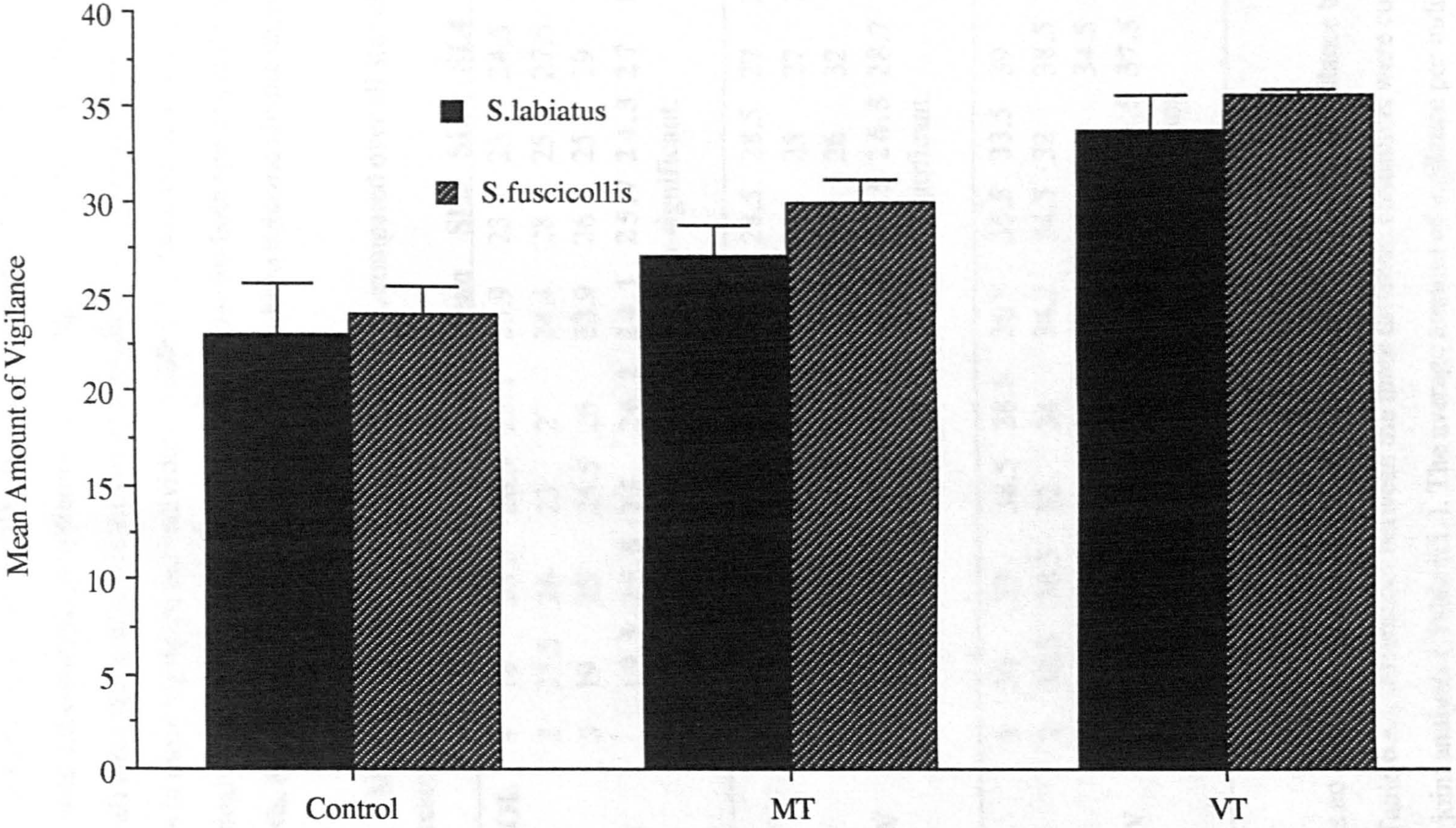


Figure 6.E : Mean amount of vigilance per individual, shown to three types of objects (Control, Mildly Threatening [MT], Very Threatening [VT]).

Overall, the mean amount of vigilance per individual was only slightly greater for *S. fuscicollis* (mean = 29.4 ; SE = 1.48), than for *S. labiatus* (mean= 28.0 ; SE = 1.02) and once again this was not significantly different (U = 8, N_a=, N_b=4, Non-significant).

In all three different conditions of objects, there were no significant differences between the species in mean vigilance per individual (Table 6.K). Each increase in vigilance caused by an increasingly more threatening stimulus was similar for both species, and it was decided that on this basis, the two species could be considered to have behaved almost identically.

Table 6.K : Mean amount of vigilance per individual, compared over all stimuli, during 15 minute threatening stimulus trials.

		SF1	SF2	SF4	SF5	Mean	SL2	SL3	SL4	SL5	Mean
CONTROL	**1**	18	25.5	26.5	25.5	23.9	23	23	24.5	12.4	20.7
	2	21.5	26	23	27	24.4	28	25	27.5	15.2	23.9
	3	19	25	25.5	26	23.9	26	25	29	17.2	23.9
MEAN		**19.5**	**25.5**	**25**	**26.2**	**24.1**	**25.7**	**24.3**	**27**	**14.9**	**24.3**
	Mann-Whitney U = 8,N_a=4, N_b=4, Non-significant.										
MT	**1**	26	31.5	30.5	34	30.5	28.5	28.5	27	26	27.5
	2	28	31	33.5	33.5	31.5	32	25	27	23.6	26.9
	3	27.5	28.5	24.5	31	27.9	31	26	32	19.6	27.2
MEAN		**27.2**	**30.3**	**29.5**	**32.8**	**30.0**	**30.5**	**26.5**	**28.7**	**23.1**	**27.2**
	Mann-Whitney U = 5,N_a=4, N_b=4, Non-significant.										
VT	**1**	36	33	38.5	38.5	36.5	35.5	33.5	39	33.2	27.8
	2	32.3	38.5	32	34	34.2	34.5	32	38.5	26.4	32.9
	3	35.3	35	35	35.5	35.2	36	35	34.5	26.8	33.1
MEAN		**34.5**	**35.5**	**35.2**	**36**	**35.3**	**35.3**	**33.5**	**37.5**	**28.3**	**31.3**
	Mann-Whitney U = 6, N_a=4, N_b=4, Non-significant.										

As no significant differences were found in mean amount of vigilance between the species (Table 6.K), differences between the three different conditions were compared in the form of a joint analysis (Table 6.L). The average amount of vigilance per individual per stimulus, was significantly greater for MT stimuli (T=36, N=8, $p < 0.05$), and for VT stimuli (T=36, N=8, $p < 0.05$), when compared to the control condition. The two threatening conditions were also significantly different, with the VT condition eliciting more vigilance than the MT one (T=36, N=8,$p < 0.05$).

Vigilance was therefore demonstrated to be linked with degree of threat, and that the two species were almost identical in the way their vigilance response increased to the presence of potential threats. Both species are therefore, not only as vigilant as each other, but they respond in a similar way to increased threats, by monitoring their environments.

Table 6.L : Wilcoxon comparison of mean vigilance shown to 3 categories of stimuli. Results are presented jointly between the species (* = significant difference , at $p<0.05$).

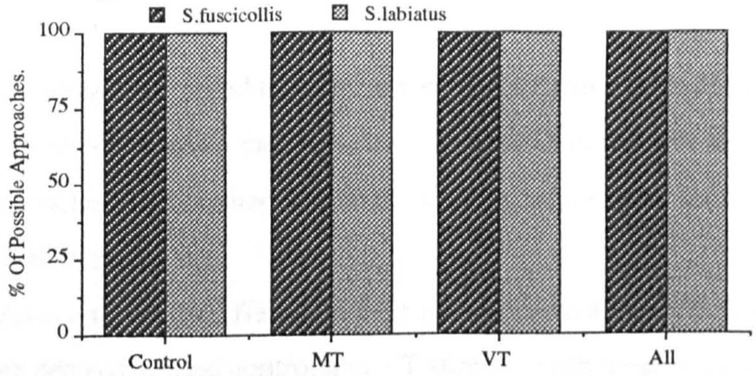
Comparison	Both
Control Vs. MT	T = 36 * (N = 8)
Control Vs. VT	T = 36 * (N =8)
MT Vs. VT	T = 36 * (N = 8)

6.11.3 Initial approaches towards stimuli.

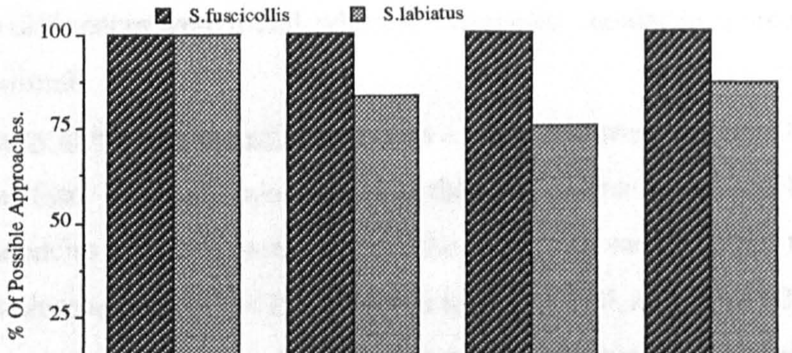
The most appropriate way of examining the results was to compare both the amount of approaches shown to stimuli in the three conditions, and the latency to complete these approaches.

a) Number of approaches ; each category of stimulus had the same number of potential approaches for each species, and so it was most appropriate to compare them as 'percentage of possible approaches'. Figure 6.F shows the distribution of completed approaches over each condition, distance and species. Both species approached to within 1m of all stimuli, in all conditions. For the 50cm category, *S. fuscicollis* approached all stimuli in the three conditions. *S. labiatus* showed a decreasing amount of 50cm approaches as the perceived threat increased. Approaches to within 15 cm of stimuli, showed a fairly similar pattern for *S. labiatus,* which approached a smaller total percentage of stimuli, but the pattern was the same as at 50cm. This time *S. fuscicollis* also followed a similar pattern of a decreasing percentage of approaches with increasing threat of stimuli. The two species differed most at control and VT stimuli, and approached a similar amount of MT stimuli.

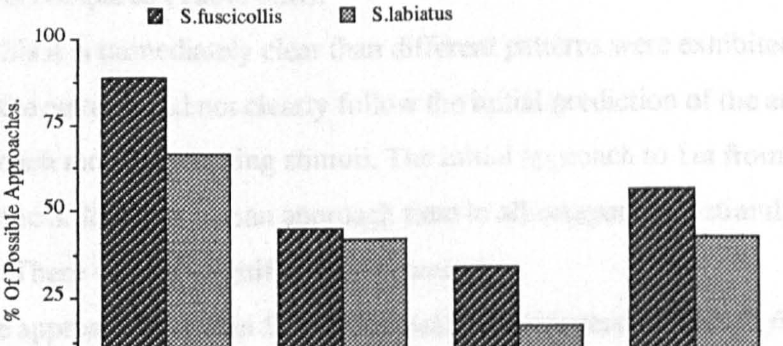
I : Approaches to within 1m of stimulus.



II : Approaches to 50 cm of stimulus.



III : Approaches to 15 cm of stimulus.



IV : Approaches to 0cm of stimulus.

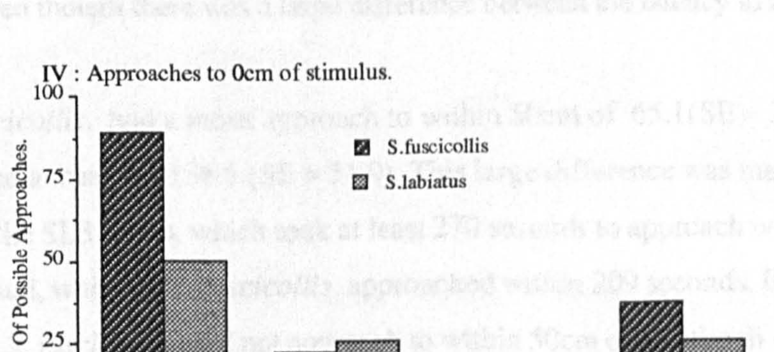


Figure 6.F : Percentage of possible approaches to four different distance categories during threatening stimuli trials.

Finally, both species failed to touch any of the VT stimuli, touched less than 1/4 of the MT stimuli, and only differed on the control stimuli. For these control stimuli, the *S. fuscicollis* approached and touched over 80% of them, while the *S. labiatus* only touched 50% of all control stimuli.

The species only really differed on their reluctance to approach close to stimuli, but differences were centred around control and VT stimuli. Both species showed a general trend towards a decreasing amount of approaching and touching stimuli, as these stimuli increased in threat. Overall differences were found, where *S. fuscicollis* tended to approach a greater percentage of stimuli.

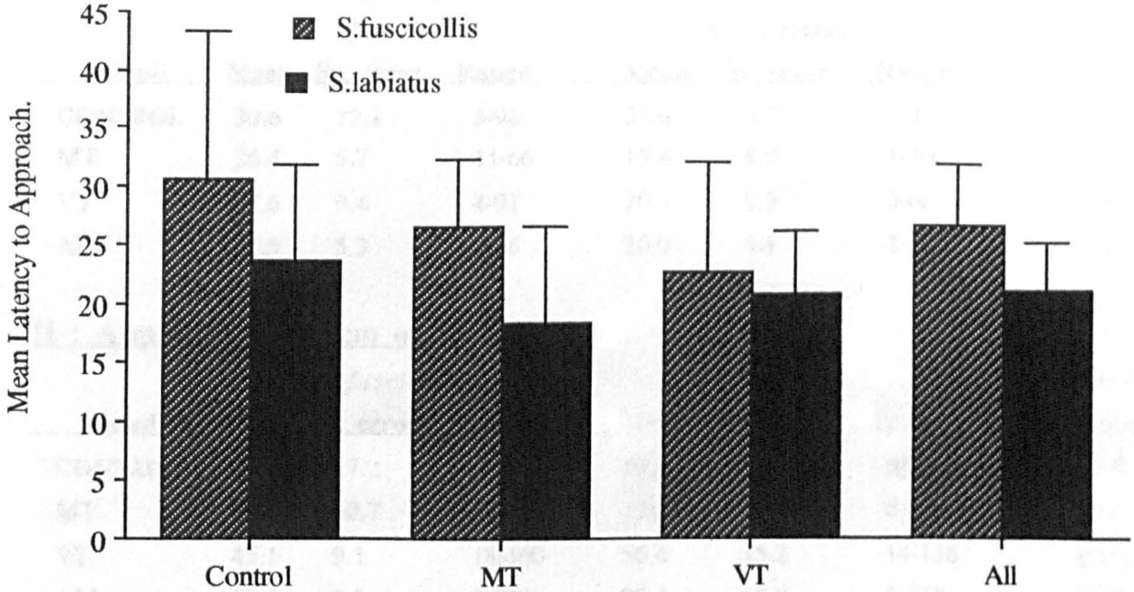
b) Latency to initial approaches ; this was a factor that was considered to be a possible way to indicate 'fear' - if the stimulus was more threatening, then it should take longer to approach it. Latencies were compared between the species for each stimulus type. However, there were few close approaches (<15cm) shown to MT stimuli, and especially to VT stimuli, so it was deemed inappropriate to calculate mean values from such a small sample size. Therefore analyses are consequently centred around the duration to approach within 1m and 50 cm, for all stimuli types. Also, mean duration to approach within 0cm and 15cm of control stimuli was also compared (Table 6.M).

From this it is immediately clear than different patterns were exhibited at the various distances, but the patterns did not clearly follow the initial prediction of the animals taking longer to approach more threatening stimuli. The initial approach to 1m from stimuli was surprising, as the *S. labiatus* mean approach time to all categories of stimuli was faster than for *S. fuscicollis.* There were no significant differences.

For the approach to within 50cm, the pattern was reversed, with *S. fuscicollis* now having a quicker mean approach (Figure 6.G). These differences were however, all non-significant, even though there was a large difference between the latency to approach MT stimuli.

S. fuscicollis, had a mean approach to within 50cm of 65.1(SE = 20.7) seconds, while *S. labiatus* had a mean of 136.5 (SE = 51.9). This large difference was mainly due to the behaviour of the SL3 group, which took at least 270 seconds to approach within 50cm of all three MT stimuli, while all *S. fuscicollis* approached within 209 seconds. It was clear however, that *S. fuscicollis* did not approach to within 50cm of all stimuli significantly quicker than *S. labiatus.*

I : Mean latency to approach within 1m of threatening stimulus.



II : Mean latency to approach within 50 cm of threatening stimulus.

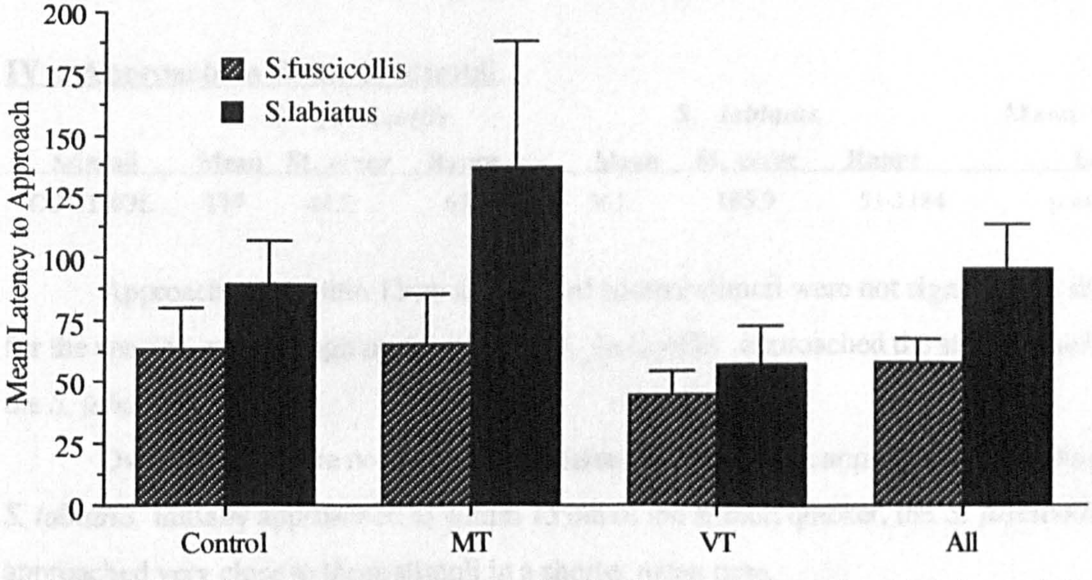


Figure 6.G : Mean latency to approach stimulus in threatening stimulus trials.

Table 6. M : Mean latency until initial approach to threatening stimuli. Latencies are mean score per area, averaged over all completed trials. (For 15cm and 0cm, only the control condition had sufficient data points for means to be calculated from).

I : Approach to 1m of stimuli.

	S. fuscicollis			*S. labiatus*			Mann-Whitney
Stimuli	Mean	St. error	Range	Mean	St. error	Range	U-test
CONTROL	30.6	12.1	5-96	23.6	8.2	3-97	p =0.19
MT	26.4	5.7	11-66	18.4	8.0	1-102	p =0.12
VT	22.6	9.4	4-91	20.7	5.3	3-66	p =0.39
ALL	26.5	5.3	4-96	20.9	4.1	1-102	p =0.28

II : Approach to 50 cm of stimuli.

	S. fuscicollis			*S. labiatus*			Mann-Whitney
Stimuli	Mean	St. error	Range	Mean	St. error	Range	U-test
CONTROL	62.8	17.2	9-169	89.4	16.4	35-209	p =0.12
MT	65.1	20.7	18-209	136.5	51.9	5-470	p =0.50
VT	45.1	9.1	18-100	56.6	15.2	14-136	p =0.24
ALL	57.7	9.3	9-209	95.1	18.8	5-470	p =0.19

III : Approach to 15 cm of stimuli.

	S. fuscicollis			*S. labiatus*			Mann-Whitney
Stimuli	Mean	St. error	Range	Mean	St. error	Range	U-test
CONTROL	116	31.9	63-310	144	62.0	50-575	p =0.17

IV : Approach to 0 cm of stimuli.

	S. fuscicollis			*S. labiatus*			Mann-Whitney
Stimuli	Mean	St. error	Range	Mean	St. error	Range	U-test
CONTROL	177	44.2	67-425	361	185.9	51-1184	p =0.24

Approaches to within 15cm and 0cm of control stimuli were not significantly different for the species, even though once again the *S. fuscicollis* approached the stimuli quicker than the *S. labiatus*.

Overall, there were no significant differences in the mean approach time. Although the *S. labiatus* initially approached to within 15 cm of the stimuli quicker, the *S. fuscicollis* approached very close to these stimuli in a shorter mean time.

6.11.4 Mean number of approaches < 75cm.

Once again the groups and species are best compared on a 'per individual' basis. Initially it was not clear whether to expect an increased or decreased amount of approaches towards frightening stimuli, as a threatening stimulus might lead to avoidance or approach. This time there was a different pattern of between the species, with the mean number of approaches per individual being different for control and very threatening stimuli (Table 6.N). Overall, there was no significant difference, even though *S. fuscicollis* had a larger mean amount of approaches (mean = 5.34 ; SE = 0.62) than *S. labiatus* (mean = 3.93;SE = 0.38). There was a tendency for the *S. fuscicollis* to approach an stimuli more times individually than the *S. labiatus* , but this was only clearly the case in very threatening stimuli, and was not clearly directed specifically towards stimuli in general.

Table 6.N : Mean number of approaches (<75cm) per individual, compared between species over all three stimuli conditions.

		SF1	**SF2**	**SF4**	**SF5**	**Mean**	**SL2**	**SL3**	**SL4**	**SL5**	**Mean**
CONTROL	1	7.3	4	1	2	3.6	2	0.5	2.5	1.6	1.7
	2	5.8	2	5	1	3.5	4.5	1.5	1.5	3	2.6
	3	2.3	5	6	6	4.8	6.5	2	1	1.6	2.8
MEAN		**5.1**	**3.4**	**4**	**3**	**4.0**	**4.3**	**1.3**	**1.7**	**2.1**	**2.4**
Mann-Whitney U = 3, N_a=4, N_b=4, p =0.08, Non-significant.											
MT	1	8	2	3	2.5	3.9	7	4.5	5.5	3.4	5.1
	2	7.5	4	6	1.5	4.8	5.5	2	7.5	2.8	4.5
	3	10	3.5	2	1	4.1	7.5	3	6	3.2	4.9
MEAN		**8.5**	**3.2**	**3.7**	**1.7**	**4.3**	**6.7**	**3.2**	**6.3**	**3.1**	**4.8**
Mann-Whitney U = 7.5, N_a=4, N_b=4, p =0.44, Non-significant.											
VT	1	9.8	5.5	3.5	6.5	6.3	8.5	2.5	5	1.8	4.5
	2	10.3	8	3.5	9.5	7.8	7.5	2.5	7	2.4	4.9
	3	10	8	3.5	10	7.9	7	3	4.5	3.6	4.5
MEAN		**10**	**7.2**	**3.5**	**8.7**	**7.4**	**7.7**	**2.7**	**5.5**	**2.6**	**4.6**
Mann-Whitney U = 3, N_a=4, N_b=4, p =0.08, Non-significant.											

As there were only 4 groups of each species and no significant differences between them, the scores of the two species were jointly analysed and compared between the three conditions (Table 6.O). The only significant difference was that the VT objects were approached significantly more times than control objects (T=34.5, N=8, $p<0.05$). Mildly threatening objects were approached more often than controls, but this was not significant (T=29, N=8, non-significant). Finally, although VT objects were approached more often than MT objects this was not significant (T=29, N=8, non-significant).

Table 6.O : Wilcoxon Test comparison of approaches to 3 categories of threatening stimuli. Results are presented jointly for both the species (Significance on Wilcoxon test, * = $p<0.05$; ns = Non-significant).

Comparison	
Control Vs. MT	$T = 29^{ns}$ (N = 8)
Control Vs. VT	$T = 34.5^{*}$ (N = 8)
MT Vs. VT	$T = 26^{ns}$ (N = 8)

6.11.5 Distance from stimuli.

This was thought to be a measure of 'relative fear' of an stimuli, where it was assumed that species would avoid close contact with stimuli that were threatening. Expected results would be that the control stimuli should generally have a greater amount of animals nearer to them than MT stimuli. The MT stimuli in turn, should have more animals nearer to them than VT stimuli. (i.e. 'perceived threat' ; VT > MT > Control). This pattern was clear in all conditions only for *S. fuscicollis* ; while although not all groups followed the exact pattern, the overall mean scores per distance did show this for all stimuli, and there was a general decrease in the number of individuals found near to the stimuli (see Table 6.P).

There was a similar general decrease in numbers as distance got closer for *S. labiatus*, but it was not perfect. For example, SL5 were found in contact with MT stimuli, more than they were within 15cm of them, and SL5 were also found within 15cm of control stimuli more than they were found in the 16-50 cm area. This demonstrates that individual groups appeared to vary their reaction to stimuli on a more individual basis, other than the 'overt threat' derived from alarm calls. The *S. labiatus* overall pattern was that which was predicted, a tendency to have lower mean number of individuals in each distance closer to stimulus as 'perceived threat' increased, and lower numbers as distance from stimulus decreased. The overall pattern can therefore be considered as similar for both species.

Table 6.P : Overall mean number of animals per group, found within 50cm of the stimulus at sample intervals (Scores are given as mean / no. of individuals, to control for group size).

I : Mean number of individuals at distance 50-16cm, from stimulus.

	SF1	SF2	SF4	SF5	mean	SL2	SL3	SL4	SL5	mean
CONTROL	4.8	1.3	1.3	1.7	2.3	1.5	0.8	0.7	1.4	1.1
MT	2.2	0	1.3	0.2	0.9	1	0	2.2	1.5	1.2
VT	1.8	0.3	0.3	1.3	0.9	1.8	0	0.2	0.5	0.6
All	2.9	0.5	1.0	1.1	1.4	1.4	0.3	1.0	1.1	1.0

II : Mean number of individuals at distance 16-1cm, from stimulus.

	SF1	SF2	SF4	SF5	mean	SL2	SL3	SL4	SL5	mean
CONTROL	2.2	0.5	0.5	0.5	0.9	0.5	0.5	0.2	3.3	1.1
MT	1.8	0.5	0	0	0.6	0	0	0.5	0.2	0.2
VT	0	0	0	0.5	0.1	0	0	0	0	0
All	1.3	0.3	0.2	0.3	0.5	0.2	0.2	0.2	1.2	0.5

III : Mean number of individuals at distance 0cm, from stimulus.

	SF1	SF2	SF4	SF5	mean	SL2	SL3	SL4	SL5	mean
CONTROL	1.5	0.5	0.5	0	0.6	0.7	0	0	1.4	0.5
MT	1.4	0	0	0	0.4	0	0	0.2	1.1	0.3
VT	0	0	0	0	0	0	0	0	0	0
All	1.1	0.2	0.2	0	0.3	0.2	0	0.1	0.8	0.3

Overall there were slightly more *S. fuscicollis* nearer to the stimulus at any distance and condition. However, there were no significant species differences found in any of the distance categories nor in any of the conditions (Table 6.Q), and it is clear that both species were as likely to be as close as each other to a threatening stimuli.

Table 6.Q : Mean number of individuals per species, found at less than 50cm from the stimulus. Comparison is between the mean number per group, for all stimuli.

I : Mean number of individuals at distance 50-16cm, from stimulus.

	Sf mean	SL mean	M-W	Number	Significance
CONTROL	2.3	1.1	U = 7	4,4	NS
MT	0.9	1.2	U = 7	4,4	NS
VT	0.9	0.6	U = 5.5	4,4	NS
All	1.4	1.0	U = 7	4,4	NS

II : Mean number of individuals at distance 16-1cm, from stimulus.

	Sf mean	SL mean	M-W	Number	Significance
CONTROL	0.9	1.1	U =7	4,4	NS
MT	0.6	0.2	U = 6.5	4,4	NS
VT	0.1	0	U = 6	4,4	NS
All	0.5	0.5	U = 4.5	4,4	NS

III : Mean number of individuals at distance 0cm, from stimulus.

	Sf. mean	SL mean	M-W	Number	Significance
CONTROL	0.6	0.5	U = 7	4,4	NS
MT	0.4	0.3	U = 7	4,4	NS
VT	0	0	U = 8	4,4	NS
All	0.3	0.3	U = 6.5	4,4	NS

Again there were no significant differences between the species (Table 6.Q), so a joint analysis was appropriate (Table 6.R). In the 50-16 cm area, only the VT objects had significantly less animals present than the control objects (T=35, N=8, p<0.05). In the 15-1cm area, both MT objects (T=27, N=7, p<0.05) and VT objects (T=27, N=7, p<0.05) had significantly less monkeys present, when compared to the control objects. However, although the VT objects had less monkeys present than the MT objects, this was not significant (T=12, N=5, non-significant). The VT objects had no moneys present at a distance of 0cm during sample intervals. Therefore, the only comparison was between control and MT objects, and although the latter had less monkeys present, this was not significant (T=19, N=6, non-significant).

Table 6.R : Wilcoxon test comparison of mean number of individuals found close (< 50 cm) to stimulus at sample intervals, shown jointly for both species. (Significance on Wilcoxon Test, * = p<0.05; ^{ns} = Non-significant).

	I : 50 - 16 cm	**II :15-1 cm**	**III : 0 cm**
Control Vs. MT	T = 28 ^{ns} (N = 8)	T = 27 * (N = 7)	T = 19 ^{ns} (N = 6)
Control Vs. VT	T = 35* (N = 7)	T = 28 * (N = 7)	-
MT Vs. VT	T = 15 ^{ns} (N = 7)	T = 12 ^{ns} (N = 5)	-

It was finally decided to amalgamate the scores of the two species, over all three distances, and to test for differences between the conditions (Table 6.S). The overall mean number of individuals found less than 50 cm from the stimulus, was significantly smaller for both MT (T=30, N=8, $p < 0.05$) and VT stimuli (T=36, N=8, $p < 0.05$), when compared to control conditions. This indicates that there was an overall tendency for the tamarins to avoid close contact with threatening stimuli.

Table 6.S : Overall mean number of individuals found less than 50 cm from stimuli. Results are amalgamated for both species, over all distances.

Comparison	Wilcoxon	Number	Significance
Control Vs. MT	T = 30	N=8	non-significant
Control Vs. VT	T = 36	N=8	$p < 0.05$
MT Vs. VT	T = 22	N=8	non-significant

6.12 Summary.

The two species behaved very similarly towards threatening stimuli, and few significant differences were found between the species. Threatening stimuli elicited more alarm calls than mildly threatening stimuli. Vigilance was found to be related to the amount of threat posed by individual stimuli, and both species showed an increase in vigilance related to an increase in threat. The two species showed a comparable and similar amount of vigilance, and the amount increased significantly with threat. The initial approaches to the stimuli showed some differences, where the *S. labiatus* approached to within 1 m quicker than *S. fuscicollis*, but at all nearer distances they were slower, or approached a lower proportion of stimuli. There was a tendency for *S. fuscicollis* to approach (< 75 cm) more times than *S. labiatus* and overall the animals approached very threatening stimuli less than controls.

This experiment highlighted the role of vigilance in the monitoring of threatening stimuli, but also demonstrated that the two species did not differ greatly in their reactions. It was also found that some of the categories used (e.g. approaches) were not very useful in determining differences between conditions and species, as responses could be both positive (i.e. animals were 'attracted' towards the stimuli) and negative (i.e. animals were 'frightened' to approach the stimuli), depending upon the perceived threat or interest in the stimuli. The difficulty in finding enough suitable stimuli / animals and the belief that a more controlled study of vigilance, and monitoring of threats was required, meant Experiment 6.2 was not carried out with mixed groups.

6.13 Experiment 6.3 ; Monitoring of threatening stimuli.

6.13.1 Introduction.

Caine (1986) showed that *S. labiatus* will make periodic checks to investigate a hidden threatening stimuli, and that the rate of checking remained fairly constant per individual, but that larger groups will have more checks per unit time, than smaller groups. This experiment investigates this idea. Initially, testing was conducted to determine if *S. fuscicollis* perform these checks, and to see if the present groups of *S. labiatus* behave similarly to those previously studied. If both groups show "checking" independently, then the roles of each species in a mixed-group can be investigated. If there is an increase in the number of checks per unit time for the mixed group, as compared to the amount shown in each group separately, then there is an advantage in active predator monitoring, and so a benefit from being in association.

Experiment 6.3 : Single species monitoring of threatening stimuli

Do both species carry out periodic 'checks' of a threatening stimulus hidden out of sight?

Are there any differences in amounts, styles or temporal patterning of "vigilance checks" ?

Prediction : If vigilance checks are a method of monitoring a potential threat, then they should increase in accordance with perceived threat, (i.e. Control objects < Non-threatening objects < Threatening objects)

6.14 Methods.

6.14.1 Subjects.

Five groups of *S. labiatus* (SL1, SL2, SL3, SL5 & SL6) and *S. fuscicollis* (SF2, SF3, SF5, SF6 & SF8) were tested monospecifically. Each group occupied their own small indoor /outdoor cage system (See Chapter 3 for specific details), and testing was carried out during May and June 1994.

6.14.2 General procedure.

The procedure initially followed that of Experiment 6.2, for the establishing of threatening stimuli. Once a stimuli was determined to be threatening, it was used in the experiment, and again the same criterion as in Experiment 6.2 was used. Three such threatening stimuli, not used previously, were selected.

The study involved the testing of vigilance checks shown to three distinct stimuli types ; a) **Control (C)** ; no stimuli was present during trial, b) **Non-Threatening stimuli (NT)** ; stimuli elicited no fear responses (e.g piloerection, alarm calling) on initial presentation and C) **Threatening stimuli (TH)** ; stimuli were selected, that elicited alarm responses in both species. Following Experiment 2 and the work of Hayes & Snowdon (1990) and Bayart & Anthouard (1992) it was decided that live animals should be used.

The order of presentation of the different categories of stimuli was randomised, and divided equally between mornings (0900-1200h) and afternoons (1300-1430h). In total, each group received 1 control presentation, and three presentations in each of the two stimuli conditions. For all stimuli, regardless of their category, the procedure was ;

(1) The animals were locked into their indoor areas, and the adjacent groups were also shut inside.

(2) Prior to each trial a brown polythene lined cloth curtain, measuring 1.5 x 1 x 1 m, was placed across one corner of the cage. The selected stimuli was either placed in the tank used for experiment 2 (TH stimuli) and was then placed on top of a 25 cm high metal stand, placed in the outside area, or was tied securely behind the curtain (NT stimuli) where both categories could only be viewed by looking above or below the curtain, or alternatively by lifting it and looking behind it.

(3) The animals were given 5 minutes to discover and approach the stimulus, and the sampling could be started if one or more individuals had found the stimulus with in this period. If it was not discovered within this period, sampling began after the first individual found the stimulus.

(4) After the initial period, the observer noted the following behaviour for a 20 minute sample session, *a) the time of each "check" of the stimuli* ; where an inspection was defined as a deliberate approach, and visual fixation on the stimuli for at least 1 second, followed by withdrawal from the stimuli. *b) the duration of the check* ; While the monkey remained in view of the stimuli, the duration of the check was noted. Only the time actually spent in visual fixation on the stimuli was recorded.

5.14.3 Stimuli.

The stimuli presented during these trials were selected prior to sampling, and were as follows ; **NT** : i) A plastic childs' windmill toy, 15cm long, ii) A plastic sheep face mask and iii) A brush head, approximately 35cm long. **TH** : i) A two-year old Californian King Snake (*Lampropeltis getulus californiae*), ii) A fourteen year old Royal Python (*Python regius*) and iii) Three adult gerbils (*Meriones ungiculatus*).

6.15 Results.

The two species were compared on their reaction to these stimuli in three different ways, i) the mean number of vigilance checks, ii) the mean total duration of vigilance per stimuli type, and iii) the mean duration per individual check (which is a function of i +ii). All are expressed as mean values per 20 minute sample session.

6.15.1 Mean number of vigilance checks.

The two species were found to perform checks of the various stimuli presented behind the screen, and these checks were more numerous during the two stimuli categories (Table 6.T).

Table 6.T : Mean number, total checking time and mean duration of checks, shown by two species of tamarins during monospecific presentations of hidden stimuli. Figures refer to mean scores per 20 minute session, and bracketed figures are standard errors.

I) A : Mean number of checks

	S. labiatus	*S. fuscicollis*	Mann-Whitney
Control	3.6 [0.5]	1.8 [0.4]	U =2.5, p<0.05
NT stimuli	6.9 [0.4]	4.1 [0.5]	U =0, p<0.01
TH stimuli	19.2 [1.5]	17.1 [0.4]	U =9.5, NS

B : Between conditions (Wilcoxon, N=5)

Control Vs NT	T=15 p<0.05	T=15 p<0.05
Control Vs TH	T=15 p<0.05	T=15 p<0.05
NT Vs TH	T=15 p<0.05	T=15 p<0.05

II) A: Mean total checking time

	S. labiatus	*S. fuscicollis*	Mann-Whitney
Control	20.4 [3.0]	8.6 [1.8]	U =2, p<0.05
NT stimuli	29.9 [3.5]	15.3 [3.8]	U =1, p<0.01
TH stimuli	164.9 [29.4]	85.3 [12.3]	U =3, p<0.05

B : Between conditions (Wilcoxon, N=5)

Control Vs NT	T=15 p<0.05	T=12 NS
Control Vs TH	T=15 p<0.05	T=15 p<0.05
NT Vs TH	T=15 p<0.05	T=15 p<0.05

III) A: Mean duration per check

	S. labiatus	*S. fuscicollis*	Mann-Whitney
Control	5.7 [0.7]	5.1 [0.9]	U =8, NS
NT stimuli	4.4 [0.6]	3.6 [0.6]	U =2, p<0.05
TH stimuli	8.4 [0.3]	5.1 [0.5]	U =3, p<0.05

B : Between conditions (Wilcoxon, N=5)

Control Vs NT	T=14 NS	T=14 NS
Control Vs TH	T=15 p<0.05	T=8 NS
NT Vs TH	T=15 p<0.05	T=15 p<0.05

Both species differed in the amount of these checks, in all conditions, the *S. labiatus* had a higher mean number of checks. This difference was significant for both control ($U=2.5$, $N_a=5$, $N_b=5$, $p<0.05$) and NT conditions ($U=0$, $N_a=5$, $N_b=5$, $p<0.01$), but not threatening stimuli trials ($U=9.5$, $N_a=5$, $N_b=5$, non-significant).

Comparing the number of checks within species, shows that both *S. labiatus* and *S. fuscicollis* increased their mean amount of checks, in accordance with threat. Both species had a significant increase in the number of checks given between Control and NT stimuli, between Control and TH stimuli and also between NT and TH stimuli (All, $T=15$, $N=5$, $p<0.05$). This trend, of an increasing number of checks being given to more threatening stimuli, was shown by both species (Pages $L(3,5) = 70$, $p<0.05$), and indicates that both species adjusted their rate of checking to correspond to the amount of alarm caused by the stimuli (Figure 6.H).

6.15.2 Mean total checking time.

In common with the number of checks, the duration of checking also differed between species and in all conditions, the *S. labiatus* had a higher mean duration of checking (Table 6.T). This difference was significant for Control ($U=2$, $N_a=5$, $N_b=5$, $p<0.05$), NT ($U=1$, $N_a=5$, $N_b=5$, $p<0.01$) and TH conditions ($U=3$, $N_a=5$, $N_b=5$, $p<0.05$). Consequently, the two species spent an increased amount of visual contact with the threatening stimuli, compared to non-threatening stimuli but *S. labiatus* spent significantly longer in visual contact during all conditions (Figure 6.H). This is once again reflected in the significant trend towards increasing duration of checking with increased threat (for *S. labiatus* $L(3,5) = 70$, $p<0.01$; for *S. fuscicollis* $L(3,5) = 69$, $p<0.05$).

Again both species had a large increase in the mean duration of checking given between Control and NT conditions, but it was significant only for *S. labiatus* ($T=15$, $N=5$, $p<0.05$). However, both species had a significant increase in the amount of checking shown between Control and TH stimuli and also between NT and TH stimuli ($T=15$, $N=5$, $p<0.05$). This indicates that both species also adjusted their total amount of checking time to correspond to the amount of alarm caused by the stimuli.

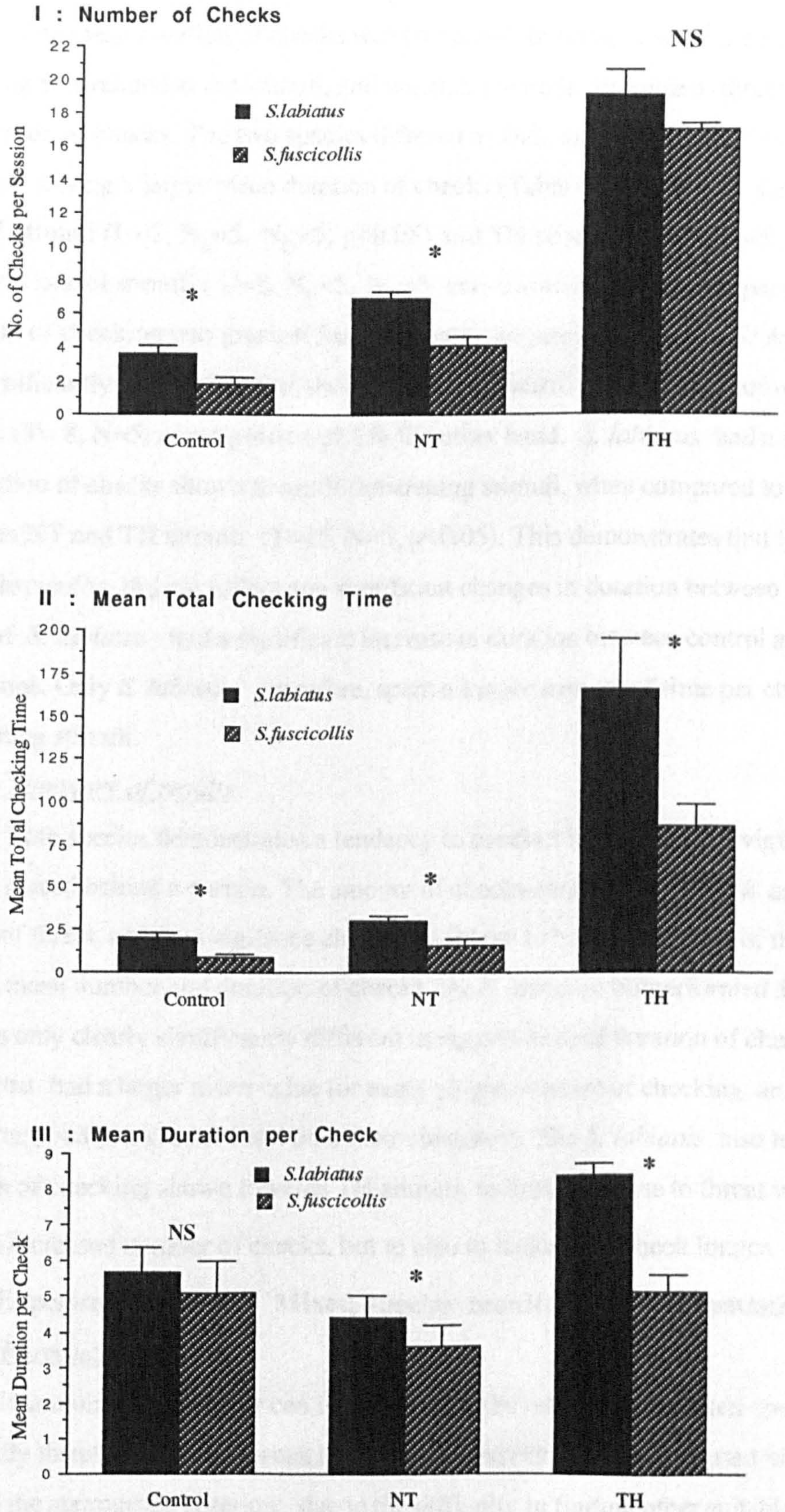


Figure 6.H : Mean number and duration of checks shown to stimuli.
(Mann-Whitney, NS = non-significant ; * = $p<0.05$)

6.15.3 Mean duration per check.

The mean duration of checks was compared, in order to see if the actual duration of checking was related to the stimuli, and whether the main response to threat was the frequency or duration of checks. The two species differed in their mean duration of checks, with the *S. labiatus* having a larger mean duration of checks (Table 6.T). This was significantly different for NT stimuli ($U=2, N_a=5, N_b=5, p<0.05$) and TH stimuli ($U=3, N_a=5, N_b=5, p<0.05$) but not for Control stimuli ($U=8, N_a=5, N_b=5$, non-significant). In both species, the mean duration of checking was greatest for TH stimuli (Figure 6.H) but for *S. fuscicollis,* it was not significantly longer than that shown to either Control ($T=14, N=5$, non-significant) or NT stimuli ($T= 8, N=5$, non-significant). On the other hand, *S. labiatus* had a significant increase in duration of checks shown towards threatening stimuli, when compared to Control and also between NT and TH stimuli ($T=15, N=5, p<0.05$). This demonstrates that the vigilance checks by *S. fuscicollis* did not reflect any significant changes in duration between conditions, but those of *S. labiatus* had a significant increase in duration between control and threatening conditions. Only *S. labiatus* therefore, spent a longer amount of time per check, viewing threatening stimuli.

6.15.4 Summary of results

Both species demonstrated a tendency to conduct brief, periodic, vigilance checks of stimuli placed behind a curtain. The amount of checks conducted, varied in accordance to the degree of threat, and thus vigilance checks are shown to be an indication of the perceived threat. In both mean number and duration of checks, the *S. labiatus* outperformed *S. fuscicollis,* but this was only clearly significantly different in regards to total duration of checking. However, *S. labiatus* had a larger mean value for every single measure of checking, and therefore was seen to respond to a greater level than their congeners. The *S. labiatus* also had an increased duration of checking shown towards TH stimuli, so their response to threat was not only to have an increased number of checks, but to also to make each check longer.

6.16 Experiment 6.3 B Mixed-species monitoring of threatening stimuli.

6.16.0 Introduction.

If stimuli that elicit fear can be found, then the reaction of a mixed-species group to a potentially threatening stimulus can be tested in captivity. The stimuli used in Experiment 6.3A fulfilled the appropriate criterion; due to the difficulty in finding other suitable stimuli it was necessary to repeat the experiment for mixed-species groups using the same set of stimuli. As it was clear that both species did indeed perform vigilance checks, this study set out simply to test two points ; i) Is there an increase in the number of "checks" of a threatening stimuli per unit time for a mixed group compared to separate monospecific groups ? ii) Do the species maintain similar rates of checks, regardless of being mixed or not ?

The first point is based on the "predation hypothesis" (see Chapter 1) which argues that a larger group should be more efficient in dealing with and monitoring potential predation threats, than smaller groups (e.g. Bertram,1978,1980; Hamilton,1971). For mixed-species groups to benefit the individuals participating in them, there should be an overall increase in the mean amount of vigilance checks per unit time, when in mixed groups. This is based on the work of Caine (1986,1987), who showed that individual vigilance checking rates in *S. labiatus* remained constant, regardless of variations in group size. Therefore, if the two species behave independently of each other, then rates of checking should not differ significantly between the conditions.

6.17 Methods.

6.17.1 Subjects.

Mixed groups, formed from five pairs of each species (GP3 : SL1 & SF3 ; GP4 : SL2 & SF5; GP6 : SL4 & SF8; GP7 : SL3 & SF6; GP8 : SL6 & SF2) were tested during this experiment. Each mixed species group was housed in a separated double indoor / outdoor cage system, and all mixed groups were separated from each other by at least one adjacent cage, containing a different species of callitrichids (see Chapter 3 for details). Testing was carried out during August 1994.

6.17.2 General procedure.

The procedure was identical to that used for Experiment 6.3A, and each mixed-species group was tested, on the same stimuli, and in exactly the same way as the monospecific trials. The only difference was that the behaviour of the two species was noted concurrently during the same trial.

6.18 Results.

Firstly, each species was compared individually, to the single species condition, to see if any significant changes had taken place. After that, the two species in mixed-species groups were compared directly in terms of , i) the mean number of vigilance checks, ii) the mean total duration of vigilance per stimuli type, and iii) the mean duration per individual check. All are expressed as mean values per 20 minute sample session.

6.18.1 Single vs. mixed-species trials.

There were few significant differences between the presentations, but both species showed a general tendency to exhibit more checks when in mixed-species groups (Table 6.U). There were only 2 significant increases, both for *S. fuscicollis* , shown to NT and TH stimuli (Wilcoxon T=15,N=5, p<0.05). In general both species did not greatly change the amount of vigilance checks they performed, when comparing single and mixed-species trials (Figure 6.I).

Table 6.U : Mean number, total checking time and mean duration of checks shown by two species of tamarins, compared between monospecific and mixed-species presentations of hidden stimuli. Figures refer to mean scores per 20 minute session, and bracketed figures are standard errors.

I) Mean number of checks (Wilcoxon, N=5)

S. labiatus	Monospecific	Mixed Species	Wilcoxon
Control	3.6 [0.5]	4.6 [0.7]	T =8.5, NS
NT stimuli	6.9 [0.4]	8.0 [0.6]	T =10, NS
TH stimuli	19.2 [1.5]	20.8 [1.3]	T =11, NS

S. fuscicollis	Monospecific	Mixed Species	Wilcoxon
Control	1.8 [0.4]	3.0 [0.6]	T =10, NS
NT stimuli	4.1 [0.5]	6.5 [1.0]	T =15, p<0.05
TH stimuli	17.1 [0.4]	19.8 [2.1]	T =15, p<0.05

II) Mean total checking time (Wilcoxon, N=5)

S. labiatus	Monospecific	Mixed Species	Wilcoxon
Control	20.4 [3.0]	15.6 [2.5]	T =10, NS
NT stimuli	30 [3.5]	35.5 [4.9]	T =11, NS
TH stimuli	164.9 [29.4]	104.5 [12.9]	T =15, p<0.05

S. fuscicollis	Monospecific	Mixed Species	Wilcoxon
Control	8.6 [1.8]	8.2 [1.9]	T =8, NS
NT stimuli	15.3 [3.8]	23.5 [5.0]	T =14, NS
TH stimuli	85.3 [12.3]	64.7 [8.2]	T =15, p<0.05

III) Mean duration per check (Wilcoxon, N=5)

S. labiatus	Monospecific	Mixed Species	Wilcoxon
Control	5.7 [0.7]	3.4 [0.3]	T =15, p<0.05
NT stimuli	4.4 [0.5]	4.4 [0.5]	T =10, NS
TH stimuli	8.4 [0.3]	5.0 [0.4]	T =15, p<0.05

S. fuscicollis	Monospecific	Mixed Species	Wilcoxon
Control	5.1 [0.9]	2.7 [0.1]	T =15, p<0.05
NT stimuli	3.6 [0.6]	3.5 [0.5]	T =8, NS
TH stimuli	5.1 [0.5]	3.3 [0.2]	T =15, p<0.05

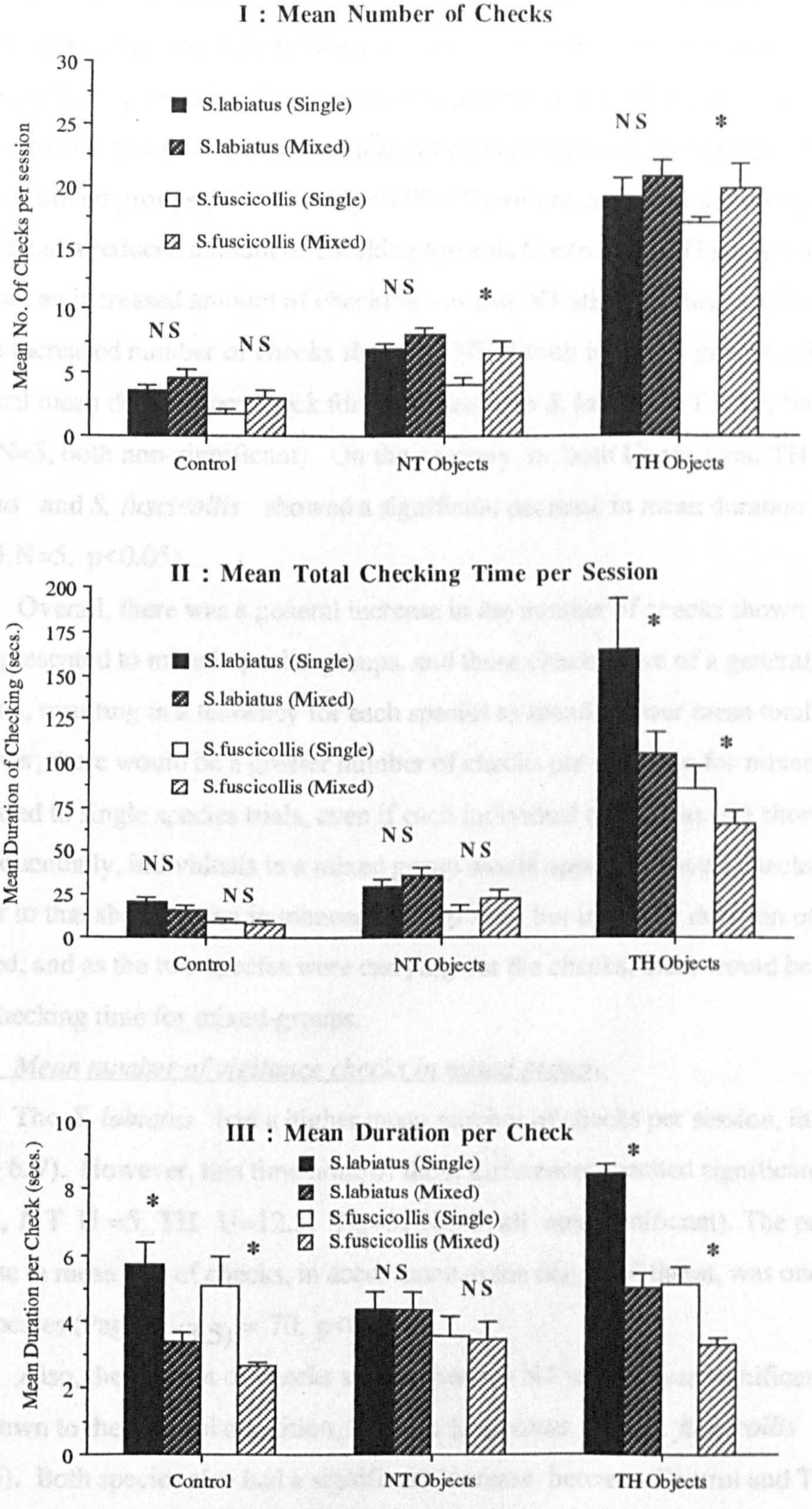


Figure 6. I : A comparison between checks in single and mixed-species groups.
(Mann-Whitney, NS = non-significant; * = p<0.05)

The mean total checking time of both species, did not change between trials. However, the total mean checking time shown towards Control stimuli actually reduced when in mixed groups, while the checking time increased significantly for NT stimuli. The only significant difference was that both species had a significantly reduced amount of time towards TH stimuli, when in mixed groups ($T=15, N=5, p<0.05$). Therefore, a pattern did emerge, where both species had a reduced amount of checking towards Control and TH stimuli in the mixed-species trial, but an increased amount of checking towards NT stimuli. This can, however, be explained by the increased number of checks shown to NT stimuli in mixed groups, added to an almost identical mean duration per check for both trials (for *S. labiatus* $T = 10$; for *S. fuscicollis* $T=8, N=5$, both non-significant). On the contrary, in both Control and TH conditions, *S. labiatus* and *S. fuscicollis* showed a significant decrease in mean duration of checks ($T=15, N=5, p<0.05$).

Overall, there was a general increase in the number of checks shown towards stimuli when presented to mixed-species groups, and these checks were of a generally shorter mean duration, resulting in a tendency for each species to spend a lower mean total checking time. However, there would be a greater number of checks per unit time for mixed groups, when compared to single species trials, even if each individual check was of a shorter duration. Consequentially, individuals in a mixed group would appear to have a checking rate that was similar to that shown when in monospecific groups, but the mean duration of checks was reduced, and as the two species were carrying out the checks, there would be a longer mean total checking time for mixed-groups.

6.18.2 Mean number of vigilance checks in mixed groups.

The *S. labiatus* had a higher mean number of checks per session, in all conditions (Table 6.V). However, this time none of these differences reached significance (**Control** $U=4.5$, **NT** $U=5$, **TH** $U=12.5$, $N_a=5$, $N_b=5$, all non-significant). The pattern of an increase in mean rate of checks, in accordance to the degree of threat, was once again found for both species (Pages $L_{(3,5)} = 70$, $p<0.01$).

Also, the amount of checks shown towards NT stimuli was significantly greater than that shown to the Control condition, for both *S. labiatus* and *S. fuscicollis* ($T=15, N=5, p<0.05$). Both species also had a significant increase between Control and TH conditions and between NT and TH conditions ($T=15, N=5, p<0.05$: Figure 6.J).

Table 6.V : Mean number, total checking time and mean duration of checks, shown by two species of tamarins, during mixed-species presentations of hidden stimuli. Figures refer to mean scores per 20 minute session, and bracketed figures are standard errors.

I) A : Mean number of checks

	S. labiatus	*S. fuscicollis*	Mann-Whitney
Control	4.6 [0.7]	3.0 [0.6]	U =4.5, NS
NT stimuli	8.0 [0.6]	6.5 [1.0]	U =5, NS
TH stimuli	20.8 [1.3]	19.8 [2.1]	U =12.5, NS

B : Between conditions (Wilcoxon, N=5)

Control Vs NT	T=15 p<0.05	T=15 p<0.05
Control Vs TH	T=15 p<0.05	T=15 p<0.05
NT Vs TH	T=15 p<0.05	T=15 p<0.05

II) A: Mean total checking time

	S. labiatus	*S. fuscicollis*	Mann-Whitney
Control	15.6 [2.5]	8.2 [1.9]	U =2.5, p<0.05
NT stimuli	35.6 [4.9]	23.5 [3.8]	U =4, NS
TH stimuli	104.5 [12.9]	64.7 [12.3]	U =1.5, p<0.05

B : Between conditions (Wilcoxon, N=5)

Control Vs NT	T=15 p<0.05	T=15 p<0.05
Control Vs TH	T=15 p<0.05	T=15 p<0.05
NT Vs TH	T=15 p<0.05	T=15 p<0.05

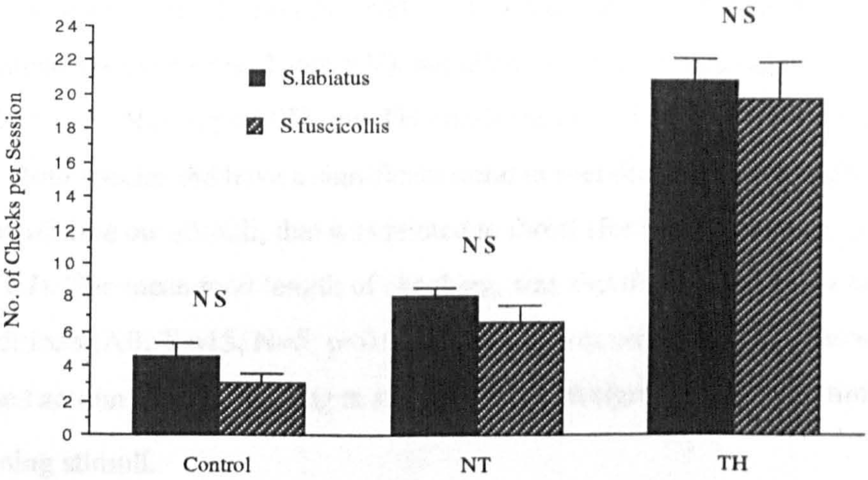
III) A: Mean duration per check

	S. labiatus	*S. fuscicollis*	Mann-Whitney
Control	3.4 [0.3]	2.7 [0.1]	U =3, p<0.05
NT stimuli	4.4 [0.5]	3.5 [0.4]	U =6, NS
TH stimuli	5.0 [0.4]	3.3 [0.2]	U =0.5, p<0.05

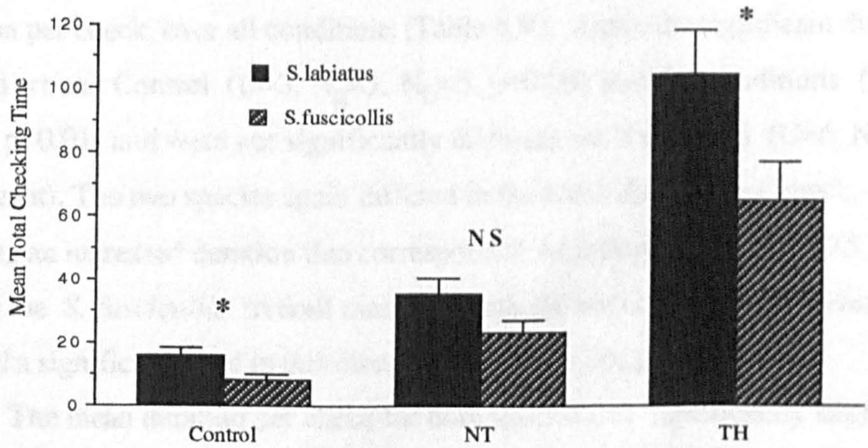
B : Between conditions (Wilcoxon, N=5)

Control Vs NT	T=15 p<0.05	T=13 NS
Control Vs TH	T=15 p<0.05	T=15 p<0.05
NT Vs TH	T=10 NS	T=11 NS

I : Number of Checks



II : Mean Total Checking Time



III : Mean Duration per Check

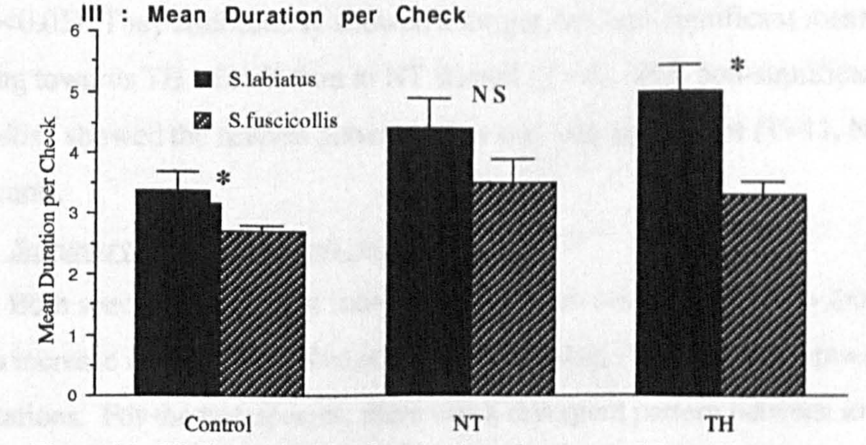


Figure 6.J : Vigilance checking in mixed-species groups (Mann-Whitney, NS = non-significant, * = $p<0.05$).

6.18.3 Mean total checking time in mixed groups.

Once again, the *S. labiatus* had a longer mean amount of time checking stimuli in all three categories of objects (Table 6.V), but differences were only significant for Control ($U=2.5$, $N_a=5$, $N_b=5$, $p<0.05$) and TH conditions ($U=1.5$, $N_a=5$, $N_b=5$, $p<0.05$).

Both species did have a significant trend in spending an increasingly larger mean duration of time on stimuli, that was related to threat (for both Pages $L_{(3,5)}= 70$, $p<0.01$: Figure 6.J). The mean total length of checking, was significantly different between all pairings of conditions (All, $T=15$, $N=5$, $p<0.05$). Both species were therefore shown to spend an increased amount of time looking at stimuli, but spent significantly more time looking at threatening stimuli.

6.18.4 Mean duration per check in mixed groups.

As with total duration and number of checks, the *S. labiatus* had a longer mean duration per check, over all conditions (Table 6.V). Again the significant differences were centred around Control ($U=3$, $N_a=5$, $N_b=5$, $p<0.05$) and TH conditions ($U=0.5$, $N_a=5$, $N_b=5$, $p<0.01$) and were not significantly different for NT stimuli ($U=6$, $N_a=5$, $N_b=5$, non-significant). The two species again differed in the mean duration per check, with *S. labiatus* showing an increased duration that corresponded with threat ($L_{(3,5)}= 69.5$, $p<0.01$), and even though the *S. fuscicollis* overall mean duration did not correspond to threat, the groups showed a significant trend in this direction ($L_{(3,5)}= 66$, $p<0.05$).

The mean duration per check for both species was significantly larger for the TH stimuli conditions, when compared to the Control condition ($T=15$, $N=5$, $p<0.05$). *S. labiatus* also had a significantly larger mean duration of checks for NT stimuli ($T=15$, $N=5$, $p<0.05$). They additionally showed a longer, but non-significant mean duration of checking towards TH stimuli than to NT stimuli ($T=10$, $N=5$, non-significant), and while *S. fuscicollis* showed the reverse pattern, it too was non-significant ($T=11$, $N=5$, non-significant).

6.18.5 Summary of mixed group results.

Both species had a slight increase in the mean number of checks shown towards stimuli, but this increase was only significant for *S. fuscicollis,* during both types of stimuli presentations. For the two species, there was a divergent pattern between total time spent checking on the two types of stimuli ; NT stimuli received a longer duration of checking when in mixed groups, while the TH stimuli received a lower duration of total checking time when in mixed groups. The Control condition also received a reduction in total checking time in mixed group trials. For the mean duration per check, the two species had a reduction when in mixed groups, during both the Control and TH conditions. On the contrary, during both trials of NT stimuli, the mean duration per check remained almost identical.

This suggests that although presentations in mixed-species trials had a reduced mean duration per check for TH stimuli, they were still checked a similar number of times, and so the mean duration spent checking the stimuli was reduced in mixed-trials. A similar pattern was found in the Control condition. However, when the NT stimuli were presented to mixed groups, they received a slight increase in the number of checks, and these checks were of a similar mean duration to single-species trials, so as a result both species had a longer mean checking time. This demonstrates that when in mixed-species groups, both species reduced their mean length of time per check for Control and TH stimuli, while keeping the mean length similar in both trials of NT stimuli. Therefore, there was no clear evidence of any habituation in response to the stimuli, as the mixed-species trials had a different effect on the mean duration of checks for the two conditions of stimuli.

For both conditions, the number of vigilance checks shown were dependent on the threat of the stimulus, the greater the threat the more checks were carried out. In all conditions *S. labiatus* had a higher mean number of checks, but this was not significant in any of the mixed-species trials, while in monospecific trials, they had significantly more checks during both the Control and NT conditions.

There was a tendency for both species to shorten their mean duration per check when in mixed-species groups. In each of the trials, the *S. labiatus* once again had a longer mean duration per check than *S. fuscicollis*, and these were significantly different for both trials of TH stimuli, for NT stimuli in monospecific trials, and for Control conditions in mixed-species trials. Again the mean length of check was related to threat, where greater threats tended to have longer mean durations per check.

The *S. labiatus* had an increased number of checks per unit time, a lower mean duration per check, and as a result had a longer total checking duration on all conditions. The total length of checking was significantly longer in all conditions of monospecific trials, and also for Control and TH conditions in mixed-species trials. The total length of checking was also related to the degree of threat, where the duration of checking increased with increases in threat.

There was evidence that individuals of both species may gain advantages when in mixed-species groups, when compared to their performance in monospecific groups. There was a general reduction in the mean duration per check for both species, during the presentation of TH stimuli to mixed-species groups, meaning that each individual in a mixed-species group spent relatively less time monitoring threatening objects. As both species were conducting checks, then the number of checks per unit time was increased for mixed-species groups.

There was also a pattern where *S. labiatus* had a higher number of checks and consequentially a longer mean total checking time than *S.fuscicollis*. For example, although TH stimuli were not checked significantly more times by *S. labiatus*, these checks were of a longer mean duration, and as a result they had a longer total time checking such stimuli. This indicates that in mixed-species groups the *S. labiatus* may have a larger contribution towards vigilance checking, as they contribute some 61% of the total duration of vigilance, even though this only represents 51% of all the total number of checks given to TH stimuli. A similar pattern occurs in both Control and NT conditions. Therefore, the two species contribute towards mixed-species vigilance checking an equivalent number of times, but the longer mean duration of checking shown by *S. labiatus* , giving a longer mean duration of checking, suggests that they may contribute more to the monitoring of stimuli.

6.19 Summary of Experiment 6.3.

It was demonstrated that the amount of vigilance checks given to a particular stimulus gave an indication of the degree of threat that this stimulus represented. Both species were shown to correspond to this pattern, and the behaviour was found in both single and mixed-species groups.

Comparing monospecific and mixed-species trials, between species, the relative amount of reaction to threatening stimuli was very similar on both occasions. Both had a similar number of checks, but *S. labiatus* had a longer mean duration per check and so conducted a longer total length of checking. This means that both species tended to conduct a very similar number of checks when separate and mixed, and suggests that the number of checks performed by a group is fairly constant over time. However, for TH stimuli, the mean duration of checks, and consequentially the total duration of checking, reduced when in mixed groups, but this presentation involved a repeated presentation of all stimuli, and so habituation to stimuli may have influenced these findings. Nevertheless, individuals of both species were shown to benefit from being in mixed-species groups, as although the number of vigilance checks shown towards threatening stimuli increased, the mean duration per check tended to reduce, and so individual contribution to vigilance checking was reduced. At the same time, there were more checks per unit time, as both species had a similar number of checks, and so a longer duration of total checking time occurred in mixed-groups.

Differences between the species on reaction to non-threatening (NT) stimuli actually reduced during mixed-species groups. For single species groups, *S. labiatus* had a significantly greater number, mean length and total duration of checks. The pattern remained in mixed groups, but the differences were reduced and none were now significant.

6.20 Overall discussion.

6.20.1 Vigilance.

Vigilance for predators may be viewed as beneficial, as it reduces the chances of an individual being preyed upon (e.g Bertram, 1978; Kenward, 1978; Lagory, 1986; Powell, 1974; Pulliam, 1973). It is however, not without cost to the individual exhibiting it, as by being vigilant they lose time which could be potentially spent in other activities, such as feeding (e.g. Abramson, 1979; Cords, 1990b; Lazarus, 1979; Lima, 1990; Sullivan, 1985). With this in mind group formation has been postulated as a way of reducing the individual contribution to vigilance, as members of larger groups can decrease their individual contribution to vigilance, without a reduction in the amount of vigilance per unit time, due to the vigilance of other group members (Alexander, 1974; Berger, 1978; Burger & Gochfiled, 1994; Lipetz & Bekoff, 1982; van Schaik & Horstermann, 1994; Terborgh, 1983; but see Lima , 1995). As the small-sized tamarins are thought to be extremely vulnerable to attack from potential predators (Cheney & Wrangham, 1987; Lindsay, 1980; Moynihan, 1970; Terborgh, 1983), then the formation of groups may be strongly dependent upon predator avoidance (see Chapter 1). Indeed, predation upon tamarins has been suggested to have exerted strong pressures on sociality, as Caine (1993 : 212) states that the "ability and willingness of tamarins to behave co-operatively, is largely a consequence of predation". This suggests that larger groups of tamarins may be more effective in predator avoidance than smaller group, since there are more eyes and ears to detect predators, while the individual group members may also benefit from a reduced level of vigilance. Evidence for such an advantage for larger tamarin groups has been found (Caine, 1984). Although not calculated explicitly, a reexamination of Caine's data, shows this pattern occurred in a study of vigilance in 2 different sized captive groups of *S. labiatus,* where individuals in a group with 3 members had a higher rate per individual, but a lower rate per unit time, than a group containing 8 members. A similar pattern was found in the current study, where the larger monospecific groups of both tamarin species had more vigilance per unit time, but generally had a lower rate per individual, than smaller groups. However, the largest group in each species had juvenile members present in them, and so it remains a possibility that any reduction in mean rate per individual was due to those juveniles not contributing as much to vigilance as adults. This may not necessarily be the case, as the youngest individual in Caine's (1984) study, which was an 8 month old juvenile, had the fifth highest rate of vigilance and this was despite the fact that all 10 other subjects were adults (> 2 years old). It may be that there is no simple relationship between age and vigilance, at least for individuals of *S. labiatus*. Nevertheless, it can be concluded that because there was a larger amount of vigilance per unit time in larger groups, then the detection of potential threats may be more efficient in these groups.

However, increases in the size of monospecific groups of tamarins may only be advantageous up to a certain size, as above this theoretical point, these groups will have additional costs in the form of feeding and breeding competition (Caine, 1993). Breeding competition will occur because usually only a single female breeds in a group, and this competition is exerted through reproductive suppression (Epple & Katz, 1984; French *et al.*, 1984). In addition, intraspecific feeding competition may become severe in large groups as the members of a species overlap totally in their feeding habits (see Pulliam & Caraco, 1984). Even though tamarins are thought to be subjected to heavy predation pressure (e.g.Ferrari & Lopes Ferrari, 1989; Heymann, 1990c; Terborgh, 1983), intraspecific feeding and breeding competition may be forcing single species groups of tamarins to form groups of a size which is lower than the optimum for maximum effectiveness in anti-predatory strategies. This is further suggested by the findings of Ferrari and Lopes Ferrari (1989), who compared the social organisation of tamarins and marmosets, and concluded that the two genera differ in their general patterns. They suggest that because marmosets have dentition specialised for gum feeding (Coimbra-Filho & Mittermeier, 1977), they can have an all year long source of predictable food, and this means they have smaller home ranges, larger group sizes and less variable social structures than the tamarins, which have a more opportunistic and less predictable diet, and have a resultant variability in group size, composition, and home ranges. This may indicate that marmosets, freed from the strong intraspecific feeding competition of tamarins, can increase their group size to better protect themselves against predators. If this is the case, then the average group size of marmoset groups (mean = 9.1; range of means, 6.6 - 11.5) may be a more optimal group size for the avoidance of predators than that of tamarins (mean = 5.5; range of means, 3.4 - 6.9 : Ferrari & Lopes Ferrari, 1989). Of course, this scenario all depends on other factors being equal, such as breeding competition, predation rate and size of animals, but these appear to be broadly similar for both genera (e.g. Ferrari,1993; Hershkovitz, 1977; Rothe & Darms, 1993; Rylands & de Faria, 1993; Snowdon & Soini, 1988). Therefore, it appears that monospecific group size in tamarins may be below that size which is optimum for predator detection, and may be constrained by intraspecific feeding competition. If this is the case, then the formation of mixed-species tamarin groups may help to give the individuals that participate in them, the improved level of anti-predator behaviour that a similarly large-sized monospecific group would give, but without the high level of intraspecific feeding competition that this would have involved (see Chapter 1; Buchanan-Smith, 1989; Peres, 1991; Terborgh, 1983). This hypothesised lack of interspecific competition is suggested by the fact that the species forming mixed-species groups tolerate each others' presence at close quarters (e.g. Heymann, 1990b; Norconk, 1990b; Peres, 1991) with little aggression, and also because both species are only aggressive towards their own species at territorial encounters (e.g. Buchanan-Smith, 1991c; Garber, 1988a; Peres, 1992b; Terborgh, 1983). Such behaviour indicates at least tolerance of their congeners by both species.

The current study gave an opportunity to gauge the effect that forming mixed-species groups would have on the vigilance of captive groups of *S. labiatus* and *S. fuscicollis.* When they were tested in mixed-species groups, both species had a significant reduction in the mean amount of vigilance per individual, while they also had a decrease in the percentage of time where there were no individuals of either species being vigilant. However, over the course of the sample period, there was more vigilance per unit time for each group. This demonstrates clearly that individuals of both species benefited from associating, as they were able to have a reduction in the mean amount of vigilance performed by each individual, but still had an increased amount of vigilance per unit time. It also conforms with the expectations outlined for the formation of groups, and suggests that both species are affected by the association, where the gain a mutual benefit in terms of vigilance for predators. This pattern has been suggested as a factor promoting tamarin mixed-species groups (e.g. Pook & Pook, 1982; Heymann, 1990c), but the current study may represent the first concrete experimental demonstration of association being beneficial to both species, in terms of a reduction in the amount of vigilance per individual in the larger mixed-species groups, while concurrently giving a larger amount of vigilance per unit time.

Another aspect of vigilance involves the nature of this vigilance, in terms of what type of predators the species are looking for. Tamarins are susceptible to a range of terrestrial and aerial predation threats (see Chapter 1, Table 1.D), and the manner of approach of these two types of predators can determine the appropriate search strategy (Terborgh, 1990). For aerial predation threats, individuals need to perform vigilance in an upwards direction, in order to spot any attacks from raptors (e.g. Peres, 1991; Price, 1990; Terborgh, 1990). This type of vigilance may be very important for tamarins, as raptors appear to be the major threat to most species of tamarins (e.g. Dawson, 1979, for *S. geoffroyi* ; Goldizen, 1987b, for *S. fuscicollis* ; Heymann, 1990c, for *S. mystax*; Neyman, 1978, for *S. oedipus*). Other types of predation threat may be spotted by a more general scanning of the environment (Caine, 1984, 1986; Heymann, 1987). Peres (1991), was able to demonstrate that *S. mystax* spent more time scanning upwards than their congeners. *S. mystax* are found at a higher mean height in the forest, and are therefore much more likely to be vulnerable to aerial predators, than the *S. fuscicollis* with which they formed mixed-species groups. A similar pattern was predicted in the current study, due to the great similarities between *S. labiatus* and *S. mystax* (see Chapter 1 ; Hershkovitz, 1977). This was clearly found to be the case, as in both monospecific and mixed-species trials, the *S. labiatus* were found to look upwards significantly more than the *S. fuscicollis*, despite the fact that neither species had significantly more overall vigilance in either condition. There was a slight tendency for *S. labiatus* to perform more vigilance overall, both monospecifically and in mixed-species groups, and a similar pattern was also found in Peres's (1991) study. If, as was the case in northern Bolivia (Chapter 2), the mean group size of *S. labiatus* is larger than that of their congeners, then the overall contribution to vigilance may be greater for *S. labiatus.* However, to date, this remains to be tested. Also, Peres (1991,1993d) demonstrated that *S. fuscicollis* performed more vigilance directed towards the lower area of the forest, and a similar pattern would again be predicted for the *S. labiatus-S. fuscicollis* mixed-species groups. Unfortunately, the small cage height in the present study (approximately 2m), meant that vigilance directed towards the lower area of the cage could not be unambiguously determined. On the other hand, the *S. fuscicollis* performed more scanning (not including looking up) than their congeners, so by nature of their lower mean height in the forest, they may be more likely to spot potential threats in the lower areas of their environment. However, this is an intriguing possibility that remains to be fully tested. Nevertheless, the pattern of vigilance in mixed-species tamarin groups are a demonstration of species-specific behaviours benefiting both members of a mixed-species group, Overall, it can be said that both species benefit from the association, in terms of the reduction in the mean level of vigilance performed by individuals of both species, when comparing single and mixed groups. However, the mean amount of vigilance per unit time is greater for these mixed-species groups, and there is less time where no individuals of either species are being vigilant. In addition, *S. fuscicollis* may gain from the increased vigilance for aerial predators shown by *S. labiatus.*

6.20.2 Reactions to threatening stimuli.

Although *S. labiatus* and *S. fuscicollis* may have both similarities and differences in all aspects of their behaviour (Chapter 1), these two species were found to have few differences in their reactions towards threatening stimuli. Both were demonstrated to exhibit a level of vigilance that corresponded to the degree of threat; the greater the threat, the larger the mean amount of vigilance. This is very important, as it shows that each species adjusted their level of vigilance in accordance with the amount of threat that each type of stimulus represented. This has been found in other studies of tamarins. For example, Caine (1984,1986) showed that for *S. labiatus*, the amount of vigilance shown to an object was related to how threatening it was,while both Moodie & Chamove (1990) and Price (1990a) have demonstrated that for *S.oedipus*, looking up is related to the level of threat from stimuli presented overhead. These are similar findings to the current study, where an increase in threat from a stimulus was shown to elicit an increased level of vigilance. Interestingly, during single species trials, there were no species differences in the levels of vigilance, and this suggests that both species were as able as each other to tailor their vigilance response to degree of threat. On the other hand, there were some slight differences in the approach behaviour of the two species, where the *S. labiatus* were quicker to approach to within 1m of stimuli but at all other nearer distances, the *S. fuscicollis* were quicker to approach. This may correspond to the tendency for *S. labiatus* to inspect stimuli visually before they approach close to them (see Chapter 5, Experiment 5.1), while *S. fuscicollis* have a greater tendency to approach and manipulate stimuli. Also, the fact that the stimuli were only 25cm off of the ground, may suggest that *S. fuscicollis* had an advantage in the actual running of the study, as they are often found lower in the cage than their congeners (Chapter 4), and may be more predisposed to approach <u>any</u> stimuli found in this area (Experiment 5.1). A similar rationale may be used to account for the larger number of separate approaches (<75 cm) made by *S. fuscicollis.* Therefore it is difficult to draw any concrete conclusions on the level of approaches made to the stimuli.

As a result, the experiment itself was difficult to control, as categories such as the number of approaches, were difficult to interpret, as a lack of approaches could potentially represent both fear (i.e. animals were frightened to approach) and disinterest in the stimulus (i.e. animals were not attracted to the stimuli). The pattern could also be ambiguous if approaches are made. For example, does an approach to an object suggest that the animal is interested and not frightened of it, or does its fear of the stimulus mean that it should "keep an eye" on the stimulus, by approaching it ?. This ambiguity, and the realisation that vigilance was the only reliable measure of interest and reaction to threatening stimuli, meant that this study was not replicated with mixed-species groups, but was modified in an attempt to study how vigilance towards threatening stimuli effects each species.

6.20.3 The monitoring of hidden stimuli.

It was demonstrated that monospecific groups gave brief, periodic vigilance checks to stimuli that were hidden from view, and that the number of such checks was related to the level of threat that the stimulus provoked. Stimuli which were threatening to tamarins (i.e. elicited alarm in the subjects) had more vigilance checks shown towards them, than non-threatening objects. This compared well to the findings of Caine (1987), on whose work the experimental protocol was based, as she had previously demonstrated that *S. labiatus* would perform periodic checks of threatening objects placed behind a curtain. The fact that monospecific groups of both species reacted to such threatening stimuli in a similar manner, means that both species have the potential to participate in the monitoring of threats. Both species had a longer mean duration per check, and a longer total duration of checking that corresponded to the degree of threat, and so the overall reaction to threat was an increase in the number and length of checks. There were species differences, however, where the monospecific groups of both species differed in their mean duration per check, the total length of checking time, and the mean number of checks. In all cases, the *S. labiatus* had larger mean values on all three conditions (baseline, non-threatening, threatening) suggesting that the *S. labiatus* had a greater level of responsiveness to all types of stimuli. Such differences may be related to life-style differences between the species (Box, 1991b), and the increased visual contact with the stimuli, may be related to the greater importance of visually directed foraging to *S. labiatus* (Buchanan-Smith, 1990a; Pook & Pook, 1982; Yoneda, 1981; also see Chapter 5). A similar pattern has been shown in the vigilance of tamarins in *S. mystax-S. fuscicollis* associations, where the *S. mystax* have a larger mean amount of vigilance than their congeners (Peres, 1993d). This suggests that the members of the *S. mystax* group (*S. imperator, S. labiatus & S. mystax*) may spend more time engaged in vigilance than the *S. fuscicollis.*

The threat of a stimulus appeared to be related to its movement, and this was similar to the findings of Hayes & Snowdon (1990), who showed that movement of stimuli caused alarm in cotton-top tamarins (*Saguinus oedipus*), and those of Jaenicke & Ehrlich (1972) who showed that both slow lorises (*Nycticebus coucang*) and greater galagos (*Galago crassicaudatus*) reacted more to live stimuli. Indeed, Masataka (1993) provides evidence that presentation of live insects to captive-bred squirrel monkeys (*Saimiri sciureus*) may sensitise a fear of snakes. The groups of tamarins in the present study had all been presented with live crickets and locusts, prior to the experiment, and so this may have helped to influence their fear of the moving stimuli, which included snakes. This monitoring of moving stimuli makes adaptive sense, as such stimuli may pose a threat at a later time due to their movement, and should be monitored until they stop being a threat, or move away.

In mixed-species trials the difference between the species was maintained, and once again the *S. labiatus* had a larger mean value on all measures. However, this time the species did not significantly differ in the mean number of checks shown towards any conditions, but *S. labiatus* spent a significantly longer time per check and had a longer total checking time during the presentation of both control and threatening stimuli. This confirms the findings of monospecific trials, and emphasises that *S. labiatus* may contribute more to the active monitoring of potential threats than their congeners. Together with the differences found in general vigilance these are indications that *S. labiatus* do indeed spend more effort in overall vigilance, and their efforts parallel those of *S. mystax* in their mixed groups (Peres, 1991, 1993d).

Both species displayed a greater number of checks when in mixed-species groups than they did in single species groups, but the increase was only significant for *S. fuscicollis* during both threatening and non-threatening stimuli presentations. However, mean duration per check decreased for both species, leading to a reduction of overall mean duration of checking. These differences may indicate that the presence of the congener influences vigilance, but it also may be due to other factors, such as habituation to the stimuli. Arguably, it is unlikely that habituation is the cause, as the number of actual checks increased, but it may be a factor in the reduction of mean duration per check, and overall mean duration of checking. However, this is unlikely to be the case for a number of reasons :

a) Caine & Marra (1988 : 900) describe the response in using threatening stimuli on two occasions, and state that "...the animals responded as fearfully as they had earlier" indicating no lessening of responses,

b) the mixed-species trials were carried out at least 2 months after the monospecific presentations, and both species usually responded to the threatening stimuli by giving alarm calls towards then upon sight,

c) the fact that the mean duration per check for non-threatening stimuli did not change between conditions, while the duration of checks towards both control and threatening stimuli conditions reduced, mean that there was no specific change in response between monospecific and mixed-species trials, and

d) the response of habituation towards novel stimuli by *S. fuscicollis* was shown to be a reduction in responsiveness to stimuli that are repeatedly presented (Menzel & Juno, 1985), while in the current study the number of checks was slightly increased.

All this evidence suggests that the results are not simply explained by a general habituation towards the objects, but are more likely to be a consequence of mixed-species groups.

The fact that the two species had only a slight increase in the number of checks, suggests that there may be a standard level of checking carried out by groups. This mirrors the findings of Caine (1987), who found that individuals in two captive groups of *S. labiatus*, one containing 8 individuals, the other having 3 members, both exhibited a similar mean number of checks per individual. The suggestion is that rates of checking are fairly constant and the main benefit of increased group size is the mean number of checks per time period and the interval between checking. Specifically, the mean interval between checks was shorter for the larger group, and they had more checking per unit time, when compared to the smaller group. In the current study, both species in the mixed-species groups had a similar number of checks, and both contributed to checking the stimulus an equal number of times. As a result, there were the same number of checks per individual, but double the number of checks per unit time, and a decreased mean interval between each check. This suggests that individuals of both species in tamarin mixed-species groups benefit from the vigilance checks of their congeners; a pattern that is mirrored in the general vigilance, and alarm calling shown by other tamarin mixed-species groups (e.g. Heymann, 1990c; Peres, 1991; Terborgh, 1983) and by individuals in other primate associations (e.g. Cords, 1990a; de Ruiter, 1986; Struhsaker, 1981).

Another benefit postulated for an increase in group size, is that individuals in larger groups may benefit from a decrease in the individual rate of vigilance that occurs with the increase in group size (e.g. Caraco, 1979; Elgar, 1989; Lendrem, 1984; Quenette, 1990), and this can be applied equally to mixed-species groups (e.g. Barnard & Thompson, 1985; Fitzgibbon, 1990; Metcalf, 1984; Morse, 1970). This was demonstrated to occur in the current study, where members of both species were found to reduce their mean duration of checking shown to threatening stimuli when in mixed-species groups. Caine (1987) did not measure this duration, so it is unclear whether she found such a pattern. However, it has been noted in several bird species (e.g. Barnard & Stephens, 1983; Beveridge & Deag, 1987; Jacobsen & Ugelvik, 1994; Lazarus, 1979) and in African ungulates (Fitzgibbon, 1990; Underwood, 1982). No study of wild tamarin groups has been able to demonstrate this, but this may be due in part to the stability of tamarin mixed-species groups, where the species are often found together for over 80% of the observation time. This makes it extremely difficult to study both monospecific and mixed-species groups in the wild. However, the present study demonstrates that the overall amount of time individuals spend in vigilance is the factor which may vary, rather than the number of actual checks which appears to be quite consistent. This does not mean that there is a lowering of the total time spent monitoring the threat, as for the mixed group as a whole, there was an increased duration of checking, when compared to each group on their own. Once again, the length per check was greater for *S. labiatus*, and this demonstrates their larger contribution to monitoring threats.

Chapter 7 : General Discussion

7.0 Overview of discussion.

The present study outlined some of the behavioural similarities and differences that occur in wild mixed-species groups of *Saguinus labiatus labiatus* and *S. fuscicollis weddelli* in northern Bolivia, and in both monospecific and mixed-species captive groups at Belfast Zoological Gardens. In this discussion, I will re-iterate the salient points of the studies described in previous chapters and will relate them to the theories outlined in Chapter 1, emphasising the possible costs and benefits involved, and demonstrating how the similarities and differences in the behaviour of each species relate to this association. Finally, I will discuss alternative theories concerning the forces driving species to associate, discuss the idea of what association really entails and also suggest further work which may help to elucidate fully the costs and benefits gained from association.

7.1 Field study in Bolivia.

Mixed-species groups of *Saguinus labiatus* and *S. fuscicollis* were examined during a 9 month field study in northern Bolivia. The proportion of time each species were observed in mixed-species groups (83% for *S. fuscicollis* ; 86% for *S. labiatus*) were similar to those found in previous studies, and the study area was occupied throughout by mixed-species groups. Several groups were studied at two main sites. The ecology of the species was compared and contrasted, and they were found to differ in mean group size, mean height used in the forest, method of locomotion, and preferred insect foraging strategies.

7.1.1 Group size.

Previous studies of group size in mixed *S. labiatus* and *S. fuscicollis* troops usually found that the mean group size of *S.fuscicollis* was greater (e.g.Yoneda,1981; Pook & Pook,1982; Buchanan-Smith,1990a), but in the present study it was found that the mean group size of *S. labiatus* was larger.

7.1.2 Serial access to resources.

Access to food trees was linked to dominance, and there was an "order effect" during feeding; the larger-bodied *S. labiatus* were generally first to enter and consume food, in middle-large feeding trees, while the smaller-bodied *S. fuscicollis* entered and fed when their congeners had departed. This suggests that *S. fuscicollis* may benefit from forming mixed-species groups, through the social facilitation of behavioural responses shown by

S. labiatus, which are related to the position of feeding resources. On the other hand, the disadvantages accrued to *S. labiatus* are minimised as they have priority of access. Many previous studies fail to mention any systematic, serial feeding pattern, where the members of the *S. mystax* group have priority of access to food resources and the *S. fuscicollis* has to wait until all or most of their congeners are finished (e.g.Garber, 1993b; Pook & Pook, 1982; Terborgh, 1983). Peres (1991) indicated that in *S. mystax and S. fuscicollis* associations, *S. mystax* were frequently first to reach the large resources, and could exclude their congeners, while Buchanan-Smith (1989) indicated that *S. labiatus* took the lead in the mixed groups, and the first *S. fuscicollis* entered feeding trees as the last member of the *S. labiatus* group left. Such a pattern was clearly found in the current study, and the *S. labiatus* often lead the *S. fuscicollis* to large resources.

7.1.3 Ecological partitioning.

In common with other studies of *Saguinus* mixed-species troops, there were both similarities and differences between the species (e.g. Norconk,1990b; Pook & Pook,1982; Terborgh, 1983). *S. labiatus* were usually found at a higher level of the forest than their congener. Both species consumed fruit at a similar height, and this reflects the large overlap in fruits consumed by both species, while insect foraging shows an important divergence between the species.

The species were shown to differ significantly in their preferred style of locomotion. *S. fuscicollis* relied upon vertical clinging and leaping for over 25% of locomotion, predominantly in the 5-10 metre area of the forest. *S. labiatus* only used this method for less than 5% of locomotion, but showed a reliance on quadrupedal running and walking, which was usually conducted along fairly large branches, in the lower and middle canopy area.

In the present study, the distribution of substrate size to height showed that *S. labiatus* predominantly used small branches in the 15-25m height band, whereas *S. fuscicollis* used mainly large substrates at a height of 0-10m. Also, the interaction between orientation and size of substrate produced a different pattern in the species. The highest ranked pairing of substrate orientation and size for *S. labiatus* was small oblique substrates, but for *S. fuscicollis* it was large vertical substrates. These divergences are intrinsically linked to the main locomotory styles used by each species, and within these pairings each species used their most common locomotory style, vertical clinging & leaping for *S. fuscicollis* and quadrupedal progression and leaping for *S. labiatus*.

In summary, substrate use during locomotion was different for each species and corresponded to the vertical stratification of these species and the type of substrates present in each area. *S. fuscicollis* use of large trunks during locomotion was tied to their use of vertical clinging and leaping to locomote, as by using their claws on these vertical substrates they can utilise substrates which are otherwise too large to use. Combined with morphological adaptations in their fore-limbs (Garber, 1991), which increase their efficiency in locomoting upon large vertically orientated substrates, allows them to utilise such trunks for insect foraging, a niche which is not used by their congeners, thereby lessening interspecific feeding competition. On the other hand, *S. labiatus* used quadrupedal progression and leaping onto small oblique substrates which they grasped and "scrambled over", and this was mainly in the middle and lower canopy area, where they concentrate on fruit and insect foraging.

7.1.4 Use of food resources.

The two species not only forage for insects at different heights, they also forage by means of different styles (Yoneda,1981,1984b). In the present study a similar pattern was found, whereby *S. fuscicollis* used a manipulative, extractive style, at an average height of less than 5 metres, while the *S. labiatus* used a visually important "seize and capture technique" looking for flying insects in, or on the foliage of the middle and lower canopy.

Both species show a convergence in the mean height used while fruit foraging, but diverged greatly in the mean insect foraging height. This probably reduces competition between the species, as insect foraging accounts for a large part of both species behavioural repertoire (e.g. Peres,1992a; Terborgh, 1983; Yoneda,1984b). There is also evidence that *S. fuscicollis* take a different set of insects than the *S. labiatus* group (Yoneda,1984a). Thus, although the potential for competition between species is high for fruit resources, the convergence in insect foraging may allow the two species to reduce the overall potential for inter-specific food competition and to co-exist amicably.

7.1.5 Conclusions of field study.

As outlined in the initial chapter, the main reasons groups are formed is in order to increase an individuals' ability to utilise and defend resources, and to counteract the threat of predation. Group formation, however, involves the participants in a series of costs, as well as benefits, and these costs are more likely to be most severe in large groups where individuals are competing for common resources. Competition can take place over fruit and insects, breeding positions and other opportunities. This is where mixed-species-groups allow the participants to receive the benefits of increased group size, without the intense intraspecific competition that would occur in similarly sized monospecific groups (see Section 1.3). In the mixed-species groups described in this field study, it is argued that ecological differences are the main factor which allow the species to be able to associate. This is because the two species differ in their mean height, and insect foraging style, allowing them to avoid each other spatially for much of the time, thus alleviating the potential for competition. However, in order for association to be beneficial for the participants, there has to be some similarities in their behaviour and ecology, so they are able to utilise and defend similar niches, and to spot similar predators. This is where the high dietary overlap between the species comes into play, and the nature of these resources ensure that there is usually a sufficient amount of the most commonly used feeding trees, in order to satisfy the dietary requirements of individuals of both species. Also, the pattern of predation upon both species of tamarin is similar, and they have an almost identical set of common predation threats (see Chapter 1). This is not to suggest that both species have an equal relationship in the association, as *S. labiatus* have priority of access to feeding trees and can control access to resources. For example, the fact that *S. labiatus* do let the *S. fuscicollis* eat after them, and there is little or no overt aggression between the species, means that the costs to *S. labiatus* of excluding *S. fuscicollis* may outweigh any potential losses due their presence. For *S. fuscicollis*, any potential costs of feeding competition due to the presence of *S. labiatus*, must be outweighed by the benefits of association, such as being led to a regular supply of food by their congeners, and in any case *S. fuscicollis* would be unable to gain possession of resources forcefully. Therefore, it appears that while in mixed-species groups, both species gain in terms of the efficient utilisation of common resources, by reducing the potential for encountering previously used resources, and thus benefiting individuals of both species.

The fact that the two species diverged in their mean height of forest used, height during locomotion, and in their preferred insect foraging strategy, allows the possibility that differences in their life-styles may lead to differences in responses in different situations. The net result could be an advantage to the participants in the mixed-species groups, as the range of reactions displayed by individuals of the different species, will give an increased level of flexibility in responses, when compared to groups of each species on their own. These reactions may be complementary to each other, as was found to be the case for vigilance in *S. mystax* and *S. fuscicollis* mixed-species groups (Peres, 1991, 1993d), where each species are alert towards different categories of potential predators. Therefore, it was hypothesised that there would be other such differences in behaviour, and this "behavioural differences hypothesis" (see Section 1.8) was investigated in the current study of captive mixed-species groups.

7.2 Captive mixed-species groups.

The idea of creating captive mixed-species groups of tamarins was a novel concept, as there have been no systematic attempts to do so, and there were no accounts previously published. After it was established that mixed-species groups of tamarins could be formed in captivity, a comprehensive study of mixed-species groups of *S. labiatus* and *S. fuscicollis*, was conducted at Belfast Zoological Gardens, Northern Ireland. These studies involved an examination of the association, and an investigation into the theoretical costs and benefits of the association, by means of a series of experiments. As outlined above, the main theoretical thrust of the study was the investigation of both similarities and differences between the species. Five mixed-species groups were created and the behaviour of the two species was compared both monospecifically and when in the mixed groups.

7.3 Ecological validity : height use, spacing and the behaviour of a free-ranging group.

Although it was established that mixed-species groups could be formed in captivity, it was necessary to examine the ecological validity of such groups, which involved a comparison of the general behaviour of captive and wild mixed-species groups, especially in terms of height use, and spatial distance between species. This was in order to determine if the behaviour of captive mixed-species groups could be empirically equated to that of wild groups.

The first part of this testing consisted of allowing one mixed-species group to free-range over a small wooded area. This procedure worked well, with both species quickly adapting to the situation, and members of the mixed-species troop were shown to be more active post-release, which was the result of a reduction in sedentary behaviour, especially resting, and a slight increase in locomotion. Similarly, both species of tamarins also showed a change in the range and pattern of positional behaviour. The *S. fuscicollis* may have been more curious, being first to venture out, covering a greater area than their congeners, but *S. labiatus* had priority, and could take advantage from the discoveries made by their congeners. Both species were found as close to each other as the average distance within same species pairs, for around half of all observations. Thus the present study found an association of at least 50% using this definition of association, demonstrating that an association was formed and not merely a tolerance of each other.

As both free-ranging species shared the wooded area, and had a coincidence in both space and time that exceeded half of observation time, it is argued that they had formed some sort of association that compared convincingly to those found in wild tamarins. This gives a degree of validity to the overall mixed-species project.

In the other section of ecological validity studies, the height use and spacing of all mixed-species groups was investigated in standard enclosures, in order to determine if the behaviour of all these captive groups resembled those of their counterparts in the wild. This was an extension of the ecological validity investigated in the free-ranging study, as time constraints meant that it was not feasible to allow all groups to free-range. All captive mixed-species groups of tamarins were found to exhibit a vertical separation in terms of mean height used in their enclosures. In *S. labiatus,* all individuals used a higher mean height of the enclosure than all the *S. fuscicollis* individuals. This pattern of vertical separation was comparable to that shown in wild groups.

The mixed group was made up of two separate groups of different species, which spent more time closer to their conspecifics than to their congeners. However, both species spent over one quarter of their time within 1 metre of each other, indicating that the members of both species were not avoiding each other. The fact that they spent this amount of time close to each other, even though the had the potential to be at least 10 metres apart, suggests that they may have formed a mixed-species group. There were a range of interactions between the species, where *S. labiatus* was clearly dominant. Overall, it can be argued that the captive mixed-species tamarin groups behaved similarly to their counterparts in the wild.

7.4 Reaction to novel objects.

In order to test the "behavioural differences hypothesis", in terms of how the two species would react to a selection of objects placed at different points of their environment, one set of studies involved the placing of novel objects in different parts of the environment. Expectations based on their vertical partitioning in the wild and in captivity, led to the prediction that the level of response may be related to the mean height each species uses in their environment.

Both species behaved as predicted, *S. labiatus* approached and touched top area objects significantly quicker, while *S. fuscicollis* approached and touched floor areas objects quicker in both conditions, and in mixed groups reacted to them before *S. labiatus* did. They also reacted to more objects overall. Objects placed in the middle of the cage were not approached or touched significantly quicker by either species. These differences in response may be related to life-style patterns under natural conditions, where the *S. labiatus* which are found at a higher mean height in the forest, reacted quicker to objects near the top of the cage, while the *S. fuscicollis,* with a lower mean height, were quicker to react to objects in the lower areas of the cage. These differences were still apparent in mixed-species trials, and it appears that the *S. fuscicollis* may lead their congeners to objects placed on the floor. The *S. labiatus* may lead their congeners to objects in the upper part of the cage, but due to their dominance, may prevent *S. fuscicollis* from approaching objects until they left. There is evidence that *S. labiatus* may use a more visually orientated approach than the *S. fuscicollis*, who were quicker overall to touch the objects after approaching them, and this may be related to their insect foraging strategies in the wild, where the *S. labiatus* use a visually orientated seize and capture, while their congeners use a manipulative, extractive foraging technique.

The *S. labiatus* are shown to exhibit a pattern of responses which mirror the behaviour of tamarins in mixed-species groups in the wild. They seem to benefit from the reactions of the *S. fuscicollis* in the lower area of the enclosures, and *S. labiatus* will contact these objects when in mixed-groups, only after they have been approached by the *S. fuscicollis.* The *S. fuscicollis* may benefit from the improved reactions of the *S. labiatus* in the top areas, although they may be forced to wait for benefits due to the dominance of their congeners. This suggests that in novel situations the "behavioural differences hypothesis" is supported, and more importantly, the presence of the associating species affects the other's behaviour and this is something which could potentially benefit each species. The cost to *S. labiatus* is likely to be low, as they can exclude the *S. fuscicollis* from any chosen resource, while the latter may have to suffer larger costs as they cannot exclude their congeners. However, as *S. fuscicollis* were still the first to react to floor objects when in mixed-species groups, the effect of competition between the species is unclear.

7.5 Reactions to food & non-food objects.

A second set of experiments investigated the ability of both species to learn the properties of objects that may or may not contain items of food, and also to determine whether the "behavioural facilitation hypothesis" could be demonstrated to benefit both species.

Captive groups of the two species were compared on their ability to learn about novel food and non-food objects while housed as single species groups, and later tested in mixed-species groups. In single species groups, both species learnt to distinguish between objects which contained food and those which did not, after a single trial. Both species were able to demonstrate a level of response that was comparable with each other, and they could retain this information for a period of at least 7 weeks.

In mixed-species groups, *S. labiatus* were first to react to objects, and their priority of access meant that the *S. fuscicollis* had to wait until their congeners had finished eating, before they gained food items. Nevertheless, they did gain some food items during every trial, and so food objects were non-monopolisable resources. This parallells how the two species exploit medium and large-sized food resources in the wild (Chapter 2), where the subordinant *S. fuscicollis* are only able to enter such feeding trees as their larger-bodied congeners departed. A similar position was found where only *S. labiatus* had prior experience about the presence of food. In response to a set of objects where *S. fuscicollis* had exclusively been presented with food, and their congeners regarded the object as containing no food, the *S. fuscicollis* were initially first to react, and the *S. labiatus* only learnt about the food through their reactions. A similar pattern was found for objects which the species had the opposite learning. This shows that behaviour concerning the presence of food can be passed between the species, and confirms that the "behavioural facilitation hypothesis" may be a relevant factor in a cost-benefit analysis of tamarin mixed-species groups. It also gives a mechanism through which the "behavioural differences hypothesis" can give benefits to the participants. This is simply the case where the reaction of one species, which may give them tangible gains (such as the food in this case), can lead to the facilitation of this behaviour in others. A similar pattern has been shown in mixed-species flocks of birds (e.g.Ward & Zahavi,1973), where one species acts as a guide to the position of food for others, and this may also be the case for tamarin mixed-species groups.

The potential costs for *S. fuscicollis* may be higher than those for *S. labiatus*, due the priority of access to resources of the latter. However, the costs of feeding competition to both species of tamarins appear to be low, as most food resources exploited by mixed-species groups of wild tamarins are superabundant and non-monopolisable (Peres, 1991). Therefore the facilitation of such behaviour certainly has little cost for *S. labiatus* as they can take any resource they choose to, while for *S. fuscicollis*, the costs of losing small resources to their congeners is also fairly low, when compared to the large amount of non-monopolisable food items which are consumed.

The overall impression is that both species are able to benefit from the facilitation of food related behaviour between the species, and this facilitation probably only has a minimal cost to both species.

7.6 Vigilance and responses to threatening stimuli.

The "predation avoidance hypothesis" suggests that individuals form together in groups in order to gain benefits, in terms of a reduction in the probability of being preyed upon (see Chapter 1). In mixed-species associations, this holds true as long as all the participating species contribute to vigilance. In addition, mixed-species groups may also have added benefits through the "behavioural differences hypothesis" allowing a specialisation of roles, with different species being alert for different types of predator. These hypotheses were examined in both monospecific and mixed-species groups of captive tamarins, where both general vigilance in absence of a threat, and active monitoring of a potential threat were tested.

In terms of the general level of vigilance, it was found that the monospecific groups of the two species exhibited a degree of vigilance, but the *S. labiatus* had significantly more looking up, and had slightly more vigilance overall. These differences were maintained in mixed groups, but the the rate of vigilance per individual was reduced, indicating an advantage for individuals in larger groups gained through a reduction in the individual amount of vigilance, while the group as a whole had more vigilance per unit time.

Both species were also shown to react to the presence of threatening stimuli by an increase in vigilance. Hidden stimuli were checked periodically, and the level and amount of checks was related to the degree of threat, the greater the threat the greater the number and duration of vigilance checks. The number of checks performed by individuals in mixed-species groups did not differ significantly from those shown by monospecific groups, but the length of checks decreased, indicating that once again the individuals of both species benefit from a reduction in the amount of time they spend checking a threat. Despite this reduction, the number of checks per unit time and total time spent checking the stimuli, was increased when compared to single species groups. Both species benefit from this decrease in individual effort, with an overall increase in total checking, but the *S. fuscicollis* may benefit more, as the *S. labiatus* had a higher number and longer mean duration of checks.

This study supports the "predation avoidance hypothesis", as the individuals forming mixed-species groups have been shown to benefit from a reduction in the amount of vigilance per individual, without a decrease in the overall vigilance per unit time. However, within this framework, the "behavioural differences hypothesis" is once again supported by the behaviour of the species, as the *S. labiatus* invested more effort monitoring for aerial predation threats. This monitoring of potential predators allows the facilitation of responses related to the danger of such threats, and due to the fact that both species respond to each others' alarm calls (e.g.

Heymann, 1990c), then such a reaction may benefit members of both species. Members of both species also gained an advantage during the active monitoring of hidden stimuli, where although the number of vigilance checks was consistent between monospecific and mixed-species groups, there was a reduction in the length of checks per individual when in the mixed-groups. This again indicates a reduction in the vigilance effort per individual, while the group as a whole had more checks per unit time. This means that members of both species invested time and effort in the checking of such threatening objects and individuals of both species experience a net gain in the amount of vigilance. On the other hand, the fact that the *S. labiatus* spent more time checking, and carried out a larger number of individual checks, means that it is possible that they may participate more than their congeners in the monitoring of threats. This remains to be tested fully, but Peres (1991) has shown that *S. fuscicollis* spend more effort looking for terrestrial predation threats than *S. mystax*. On this basis, it could be argued that complementary anti-predatory behaviour may be an important factor in the evolution of tamarin mixed-species groups, especially in light of the suggestion that tamarins are subject to high predation pressure (e.g. Caine, 1993; Cheney & Wrangham, 1987). If this is the case, then it highlights a clear example of how behavioural differences can lead to benefits for the participants of mixed-species groups.

7.7 The potential costs and benefits of *S. labiatus*-*S. fuscicollis* associations.

In order to examine fully the nature of *S. labiatus* - *S. fuscicollis* mixed-species groups, it is necessary to amalgamate the results of the present study with those of other tamarin mixed-species groups, and to propose a set of costs and benefits that affects each species when in association. These costs and benefits are examined on two different levels;

a) those that individuals belonging to groups of each species would receive when in a mixed-species group, compared to those they would receive when in a similarly sized monospecific group, and

b) a comparison of the relative costs and benefits to each species due to the presence of their congeners. Both levels are jointly discussed below, but all costs and benefits are separated into two sections, consisting of immediate (day-to-day) and long-term costs and benefits.

7.7.1 Immediate costs and benefits.

Immediate costs and benefits are those which may be examined on a day-to-day level, and have formed the basis for the investigations in this thesis, and also in most other studies of tamarin mixed-species groups (e.g. Buchanan-Smith, 1990a; Peres, 1991; Terborgh, 1983). The potential costs are explored in terms of : i) the competitive effect individuals of each species have on their congeners, ii) the costs which are involved with maintaining the association, and iii) the costs of territorial defence. Benefits are examined as three separate concepts : i) the facilitation of responses between individuals of both species, ii) the use of food resources, and iii) improvements in anti-predator vigilance.

The discussion will continue the approach adopted throughout this thesis, whereby species differences are emphasised. An overall synthesis of the potential costs and benefits of forming tamarin mixed-species groups, is presented in Table 7.A. The costs of association will be considered first.

Costs.

i) Feeding Competition.

The degree of feeding competition shown between individuals of both species in tamarin mixed-species groups has been shown to be a function of the size of resource involved (Peres, 1991). In large-sized feeding trees, which contain sufficient food for both species, the two species do not compete for access to the resource, but in small-sized trees, which could be monopolised by one species, there may be conflict between the individuals forming tamarin mixed-species groups (see Chapter 1). When such small resources are encountered, the dominance of the *S. mystax* group allows them to take control of the resources, and they are able to prevent their congeners from consuming food until they were satiated (Norconk, 1990b; Peres, 1991). In the present study it was demonstrated that the *S. labiatus* did, however, have some small losses due to the presence of their congeners, as the *S. fuscicollis* ate some food in most circumstances, and so took resources which could be potentially utilised by *S. labiatus.* A similar pattern was found in both the wild groups in Bolivia (Chapter 2) and in the food/non-food experiments (Chapter 5). Therefore the costs of feeding competition to *S. fuscicollis* may be greater, as they can be out-competed by their congeners through both exploitative and interference competition. However, the effects of feeding competition on both species are likely to be minimal, due to the fact that most of the shared plant food resources used by tamarins are relatively large and non-monopolisable, enabling both species to gain sufficient items of food (e.g. Garber, 1993b; Peres, 1991). Indeed, Garber (1988a) has data which show that increases in the group size of *S. mystax* which were part a mixed-species group, led to no significant increases in overall day range, foraging costs, nor feeding competition, suggesting that inter-specific competition did not place high demands on the participants. Nevertheless, the threat of competitive exclusion by their larger congeners, remains a potential cost for the smaller bodied *S. fuscicollis* (Table 7.A).

Table 7.A : Possible costs and benefits involved in mixed-species tamarin groups.

	S. labiatus	*S. fuscicollis*
Costs		
Feeding Competition	(1) Lose some food to *S. fuscicollis* through exploitative competition.	(1) Lose food to *S. labiatus* through exploitative competition, and also through interference competition, as they are dominated by their congeners.
	(2) Increased travel costs when in mixed-species groups.	(2) Increased travel costs when in mixed-species groups.
Maintenance of Association.	(1) Long calls to *S. fuscicollis*	(1) Long calls to *S. labiatus*
Territoriality		(1) Reduction in feeding / foraging until *S. labiatus* encounters are over.
		(2) May have to move if *S. labiatus* lose in territorial encounters.
Benefits		
Facilitation of Responses	(1) Can exploit the reactions of *S. fuscicollis.*	(1) Can exploit the reactions of *S.labiatus.*
Use of Resources	(1) Can monopolise small resources discovered by *S. fuscicollis.*	(1) Led to resources whose location are known to *S. labiatus.*
	(2) Effective monitoring / use of plant food resources.	(2) Effective monitoring / use of plant food resources.
		(3) May benefit from successful territorial defence by *S. labiatus.*
		(4) Can capture insects displaced downwards by the foraging of *S. labiatus*
Improved Vigilance	(1) Gains in vigilance per unit time	(1) Gains in vigilance per unit time.
	(2) Reduction in mean vigilance rate per individual.	(2) Reduction in mean vigilance rate per individual.
	(3) Benefits from the monitoring of terrestrial threats by *S. fuscicollis.*	(3) Benefits from monitoring of aerial predation threats by *S. labiatus.*

There may also be another set of costs, which are dependent upon the presence of congeners. Terborgh (1983) was able to study a group of *S. imperator* when monospecific and when in a mixed-species group, in the same territory. He did not find any effects on the number of feeding trees visited, but *S. imperator* were found to travel around 30% more, when in mixed-species groups. Terborgh (1983 : 181) suggested that exploitative competition from the *S. fuscicollis* (consuming potential resources found nearby), means that the *S. mystax* may have to travel further to find the next resource. If such an effect occurs in *S. labiatus-S. fuscicollis* mixed-species groups, then this is another potential cost to *S. labiatus*. There is no available evidence on *S. fuscicollis* when "in and out" of association, but it is a distinct possibility that such an effect is also found in this species.

ii) Maintenance of Association.

Both species in all tamarin mixed-species groups have been described as participating in the maintenance of associations (Buchanan-Smith, 1990a; Norconk, 1990b; Terborgh, 1983), which is usually achieved through mechanisms such as antiphonal long calling (Pook & Pook, 1982), early morning long calls (e.g. Heymann,1990b), backtracking and calling when separated (Terborgh,1983; Buchanan-Smith, 1989) and choosing sleeping sites which are relatively close to each other (usually <100m : Buchanan-Smith, 1989). These actions are presumably not without cost. For example, the intense long-calling of both species may be energetically costly and may also alert potential predators to the presence of the caller. In addition, back tracking and waiting until the other species appears, as well as all the long-calling, are costly to both the species participating in mixed-species groups, as they are spending valuable time and effort in maintaining the association which they could be spending in more productive behaviours such as feeding and foraging. Therefore it appears that members of both species sustain costs in the maintenance of the association.

iii) Territoriality.

Garber (1987: 355) indicates that another factor which should be considered in the determination of the cost and benefits of association, is the fact that both species appear to "jointly defend" resources from other mixed-species groups. This can be best described as parallel territoriality, as both species were found to interact only with their own species, but encounters usually occurred between both sets of conspecifics at the same time. In another more detailed report, Garber (1988a : 32) described a situation where a larger *S. mystax-S. fuscicollis* mixed-species group were better able to defend resources from smaller mixed-species groups, and he proposes that there "may exist a positive and important relationship between troop size and successful resource defense". However, an examination of his data show the main demographic change was that the number of adult and sub-adult *S. mystax* reduced by 5 animals, from 9 individuals to down 4, while those of the *S. fuscicollis* remained constant at 6 individuals. This suggests that the competitive ability of only the *S. mystax* may be the pertinent factor in defence of territories. In support of this suggestion are the data of Peres (1992b), who suggests that *S. mystax* invest more effort in territorial defence, having more physical contact, receive more injuries, and have a higher frequency of such encounters than their congeners. He also states that *S. mystax* determine the timing and direction of intergroup approaches, and that *S. fuscicollis* may be "enjoying a protective shadow against resource depletion....... provided primarily by moustached tamarin's greater effort in range defence" (Peres, 1992b : 243). This notion remains to be tested fully, but if the competitive ability of *S. mystax* is the factor which determines the successful defence of a resource (which is likely due to their dominance over *S. fuscicollis*), then *S. fuscicollis* may be open to potential losses when these congeners are unsuccessful in resource defence. Costs of loosing a territorial encounter include an increase in the mean daily path length, a reduction in time spent resting and an increased distance required to travel to the next feeding tree (Garber, 1988a). In addition, even when *S. mystax* are carrying out their frequent territorial encounters, and *S. fuscicollis* are not having such encounters with their conspecifics, there is still a potential cost to *S. fuscicollis,* as they usually spend more time resting during encounters, "watching moustached tamarins chase each other" and as a consequence they spend less time eating or foraging, when compared to their behaviour when outside encounters (Peres, 1992b: 233). This indicates that the *S. fuscicollis* are open to potential costs of territoriality, even when they themselves are not defending resources, due to the unsuccessful defence of that resource by their congeners. It also means that the results of the territorial encounters between groups of *S. fuscicollis* may be unimportant in the defence of important resources. This is because even if a group of *S.fuscicollis* wins, the simultaneous loss of a territorial encounter by the group of *S. mystax* with which they are forming a mixed-species group, will lead to a withdrawal of that *S.mystax* from the contested area (Peres, 1991). Such a withdrawal will also affect the *S. fuscicollis,* as due to the dominance of the *S. mystax,* and their ability to exclude any group of *S. fuscicollis* from resources, means that whether or not the *S. fuscicollis* group wins, the "winning" group of *S.mystax* will control the resource. Also, the cohesion of mixed-species groups suggests that the associated group of *S. fuscicollis* will be forced to depart with these losers. Therefore, the actions of *S. fuscicollis* may have little importance in the defence of resources, but they are open to the costs of the unsuccessful territorial defence by their associated congeners.

Benefits.

The advantages of forming mixed-species groups, are now examined in terms of the day-to-day benefits that individual members of each species of tamarin may receive from forming associations with their congeners (Table 7.A).

i) Facilitation of Responses.

The actions of one species have been demonstrated to influence those of their congeners (Chapter 5), and these actions may also bring about the facilitation of behavioural responses between individuals of both species. There may be differences between the species, in the way they react to any specific situation. This forms the basis of the "behavioural differences hypothesis" which was tested throughout this study, and the information transferred can take various forms. For example, behaviour may relate to the warning of potential threat through facilitation of responses to threatening stimuli (Heymann, 1990c), and it can also take the form of informing others about the presence of food. Both types of facilitation may occur as the result of differential responsiveness to stimuli or situations in different areas of the environment (e.g. baited traps in the lower forest, see Buchanan-Smith, 1989; Novel objects, Chapter 5, Section 5.1). Such facilitation may occur between either species, depending upon the situation, and both species are potentially able to benefit from the behaviour and reactions of their congeners (Table 7.A).

ii) Use of Resources.

The current study also indicated that both *S. labiatus* and *S. fuscicollis* are able to learn about the location of food sources from the behaviour of their congeners, and individuals of each species are able to use such behaviour, provided the food source is too large to be monopolised by only one species. The *S. labiatus* may benefit more from such situations, as their dominance allows them to take control of the resources, thus preventing their congeners from consuming food until they departed. For example, Peres (1991) has shown that *S. mystax* are able to monopolise small resources which are found by *S. fuscicollis*, and they therefore receive the benefit of this "piracy" of such food items from *S. fuscicollis.* However, because the majority of food items used by both species of tamarin in mixed-species groups, are large non-monopolisable resources, then individuals of both species are able to gain sufficient items of food. It has been found that members of the *S. mystax* group lead the *S. fuscicollis* to the position of such large feeding trees (Chapter 2; Buchanan-Smith, 1989;

Peres, 1991) and so they too benefit from the actions of their congeners.

As the two species have been shown to share a common territory, travelling together for most of the time, and utilising a large proportion of the same resources (see Chapter 2; Buchanan-Smith, 1990a; Pook & Pook, 1982), then it appears that the mixed-species groups behave in a manner which allows the efficient monitoring and use of resources within this territory (Gartlan & Struhsaker, 1972). This is another area which may benefit both species, as it may minimise the amount of travel time, if the species travel efficiently between feeding trees (see Garber, 1989; Garber & Hannon, 1993), and reducing the chances of encountering resources which have been previously depleted by the other species. This is the case, especially if we consider the potential for competition between the two species, if they were living monospecifically and independently, in the same territory, and utilising many of the same resources. In such a case, the chances of encountering areas that had been previously used by the other species, would be much higher, and this could lead to an increase in the amount of travelling to find resources, an increase in the amount of "wasted journeys" to previously exploited areas and could lead to more severe interspecific aggression over resources. All these problems could be reduced if the two species systematically exploited their resources at the same time. Although, there are also increased travel costs which each species exerts on their congeners (see Costs), the relative effect of these may be lessened when the species form mixed-species groups. This is because the two species are competing for resources, whether they associate or not, but if they do associate together, they can effectively minimise any wasted journeys, relative to the potential amount of travel they would perform when moving independently. Therefore, it appears that jointly utilising resources may be a benefit for both species in a mixed-species tamarin group.

It has been suggested that it is the actions of *S. mystax* which are the principal factor which determines the successful defence of a resource (see Costs), and the *S. fuscicollis* are forced to bear costs when the *S. mystax* that they are associated with lose in territorial encounters. If this is the case, then it is logical to assume that they may also benefit when their congeners are the winners in such an encounter. This allows *S. fuscicollis* in mixed-species groups the opportunity to benefit from the resource defence actions of their congeners, but also allows them to be open to potential losses when these congeners are unsuccessful in resource defence.

Finally, Peres (1992a) has demonstrated that *S. fuscicollis* are able to gain an advantage from forming mixed-species groups, in terms of insect prey items. Specifically, the visually orientated foraging of *S. mystax* creates a disturbance in the lower and middle canopy areas of the forest, and this leads to the displacement of some large insects downwards. This is an indirect action of the foraging, and the potential costs to *S. mystax* are low, because the insects being displaced are probably ones they would not catch anyway. On the other hand, these insects are readily consumed by *S. fuscicollis*, and represent a benefit of association for this species.

iii) Improved Vigilance.

The costs and benefits of association for each species are not identical, and may represent compromises between anti-predator behaviour and feeding efficiency. In the current study, it was found that individuals of both species had a reduction in the level of vigilance per individual, but an increase in the amount per unit time, when forming mixed-species-groups (Chapter 6). This shows that individuals of both species clearly gain anti-predatory benefits from being in association. These benefits may be asymmetric, as the *S. labiatus* carried out more vigilance checking, had a longer mean time per check, and performed more looking up than their congeners. Indeed, this may be very important when it is remembered that *S. labiatus* had a larger mean group size at the study site in Bolivia, so they probably perform a larger proportion of all vigilance checks than their congeners do. This suggests that a greater cost of vigilance may be borne by the *S. labiatus.* On the other hand, as *S. fuscicollis* have been shown to scan for predation threats in the lower part of the forest while in other associations (*S. mystax-S. fuscicollis* groups : Peres, 1991), and because they occupy a lower mean height than *S. labiatus,* then it is feasible that they behave in a similar manner in the current associations. If this is the case, then the combination of *S. labiatus* looking upwards for aerial threats, and *S. fuscicollis* scanning for terrestrial threats, could give a very effective pattern of complementary behaviour. This remains to be tested empirically, but individuals of both species clearly benefit from the general vigilance behaviour of their congeners.

7.7.2 Long-term benefits.

The evaluation of the costs and benefits of forming tamarin mixed-species groups which is presented above, only deals with those actions which immediately affect the participants. It is now appropriate to consider some of the long-term benefits that may be gained from association.

Breeding Competition.

Both Buchanan-Smith (1989) and Peres (1991), have independently suggested a different mechanism through which both tamarin species may benefit from the formation of mixed-species groups. Both focus on the breeding system of tamarins, and the high energetic costs of successfully rearing offspring. Female tamarins produce twin offspring, which are a large size when compared to the females' own bodyweight (Leutenegger, 1973), and these infants require to be almost constantly carried over their first few weeks of life (e.g. Epple, 1975; Price, 1990a; Pryce, 1988; Tardif, 1984). The costs of feeding and lactation mean that helpers are usually needed to rear offspring successfully (Goldizen, 1987b; Snowdon & Soini, 1988). Infant care is often provided by males, involving both direct (e.g. carrying, food sharing) and indirect (e.g. territorial defence, vigilance) types of care (Snowdon & Suomi, 1982), and this suggests that multiple males may be a "critical component of the reproductive viability of groups" (Peres, 1991 : 200). The females' heavy investment in offspring, and the need for potential help from males, means that these males may be a resource which they compete for. This is supported by the inhibition of reproduction of other females by the dominant, breeding female in captivity (e.g. Epple & Katz, 1984 for *S. fuscicollis*), and the finding that wild groups are usually found to contain only a single breeding female (e.g. Buchanan-Smith, 1990a; Garber *et al.*, 1984; Peres, 1991; Terborgh, 1983). This means that only one female is able to breed within a group, and an increase in group size would lead to an increase in the number of reproductively redundant group members. This would affect the sexes differently, and females would be the most strongly hit, due to exclusivity of the female breeding potential, while any number of males may have the opportunity to mate. While there remains the possibility that non-breeding group members can gain through inclusive fitness (Hamilton, 1964), by helping to rear closely related infants, the benefit of this will depend on the degree of relatedness, and this may be uncertain, especially if mating systems are polyandrous (Goldizen, 1987a,b; 1989). Also, it is unlikely that offspring breed in their natal group, unless there is a change in the breeding female. Therefore a large monospecific group may not be attainable, possibly due to severe sociosexual conflict, meaning that monospecific groups are subjected to breeding system constraints which gives them a maximum group size that is below the optimal size for predator detection, avoidance or other benefits of sociality.

In support of this contention, Peres (1991) has argued that the group size of tamarins which live monospecifically and in mixed-species groups are virtually identical, suggesting that such breeding constraints may be forcing limitations on the size of tamarin groups. The formation of mixed-species groups, allows two such single species groups to join together, giving individuals of each species an opportunity to enjoy all the advantages of larger group size, without the increased breeding competition similarly sized monospecific groups would face. A similar rationale is applied by Buchanan-Smith (1989), who argues that the 'optimal' group size for tamarins in mixed-species groups may be smaller than that of monospecific groups. She argues that, through the sheer increase of numbers, individuals in mixed-species groups can experience the same anti-predatory benefits as large monospecific groups. Buchanan-Smith, further argues that individuals in mixed-species groups may benefit from a greater opportunity to breed, due to a reduction in the number of individuals competing for breeding positions, when compared to individuals living in large monospecific groups. In summary, Buchanan-Smith (1989) has suggested that the optimal group size of tamarins within mixed-species groups may be smaller than those in monospecific groups, giving an increase in the number of individuals gaining breeding status, while Peres (1991) has argued that breeding constraints have forced a maximum intraspecific group size for all tamarin groups, and individuals in mixed-species groups gain in terms of predator avoidance and feeding efficiency. Both authors agree that individuals of both species may also gain through other benefits such as reduced competition and improved predator detection. In effect, individuals belonging to the two groups may gain in the long term, through benefits such as improved survival and breeding success, due to the increase in overall group size, when compared to the levels found in groups of a similar size living monospecifically.

The effects of association on group size has yet to be tested empirically, as the data set available on group size is incomplete, and are derived from a variety of different sources, using different techniques, so their accuracy is questionable. Only detailed studies concerning the composition of tamarin groups, the degree of relatedness of group members, the potential reproductive strategies available for both sexes, and immigrations and emigrations from social groups, will help to clarify the sociosexual parameters which determine group size. Also, long-term comparative data on survival and breeding success for species and groups which are found monospecifically and in mixed-species groups are needed. Until this data is available, the relevance of such parameters to the various costs and benefits of forming tamarin mixed-species groups are still unclear.

Increase in population density for *S. fuscicollis* when in mixed-species groups.

Norconk (1990b) has argued that the population density of *S. fuscicollis* is greater that those of their congeners, and that the population density of *S. fuscicollis* is greater within mixed-species groups, compared to that in monospecific groups. This evidence suggests that the *S. fuscicollis* are benefiting from being part of the association, perhaps by having a lower level of interspecific competition or a lower predation rate than monospecific groups. It allows for the possibility that *S. fuscicollis* may have greater survival of offspring, a greater access to scarce resources, or some other benefits not available to monospecific groups. However, these findings have to be placed into perspective, as they are contradictory to those of the present study (Chapter 2), where *S. labiatus* had a larger mean group size (and population density) than *S. fuscicollis*, so once again only detailed field studies, using common methodology will elucidate the position. Also, the validity of Norconk's (1990b) assumptions are questionable, as her data set includes data from "cropped" populations, that have been subjected to the trapping and removal of animals (e.g. Glander *et al.*, 1984; Ramirez, 1984), and in some of the other studies were from areas where extensive trapping had occurred. For example, Pook & Pook's (1982) study was at a site where *S. labiatus* had previously been removed (Galindo Franco, pers. comm.), and this could partly explain the results. However, it remains a possibility that could be explored only through field studies, using common methodology.

Overall, the long-term benefits of tamarin mixed-species associations are unclear, and difficult to quantify, so their contribution to the formation of mixed-species groups is unknown. Nevertheless, they remain factors which should be considered in the determination of the costs and benefits of mixed-species groups, and could be a focus for future studies.

7.8 Possible future studies.

The present study has not only helped to elucidate some of the possible costs and benefits of tamarin mixed-species groups, but has also lead to the opening up of several potential areas for further investigation, and some of these are now examined. The ensuing discussion will be split into 2 separate sections, one dealing with studies on captive mixed-species groups, the other involved with studies of wild tamarin groups.

7.8.1 Captive studies.

Long-term monitoring of captive mixed-species groups.

As the formation of tamarin mixed-species groups in captivity was a relatively new phenomenon, and was shown to work for a period of at least 1 year or more (Hardie *et al.*, 1993), it remains an interesting proposal to study such groups over a much longer timescale. Investigations could be centred around parameters such as spatial relations and degree of association, looking at whether or not the degree of association changes with time, whether the mean inter-specific distance changes over time, and whether or not such groups are stable over a much longer period of time. One interesting line of investigation could be to look at the effect of female reproductive cycle on the association, as Heymann & Sicchar Valdez (1988) found that this had an effect on the degree of association and level of interaction in a captive mixed-species group of *S. mystax-S. fuscicollis*. However, the most important factor to study would be the ability of both species to be able to breed in their mixed-species group. This is vitally important if the number of subjects in such groups is to increase, and at its simplest, if the presence of one species prevents the other from breeding, then mixed-species groups are not a suitable method for keeping captive tamarins. It would also be interesting to see if each species reacted to the presence of infants, in either an aggressive or friendly manner, or do they try to carry the other species' infants, as was the case in some other captive mixed-species groups (e.g. Xanten, 1992). Such data are required in order to ensure that mixed-species groups are actually good (or at least are not detrimental), for the welfare of captive tamarins

A final possibility involves the formation of a three-way mixed-species group in captivity. This could be formed between *Callimico goeldii* and *S. labiatus & S. fuscicollis*, as they have been found to associate in northern Bolivia (Buchanan-Smith, 1989; Christen & Geissmann, 1993; Pook & Pook, 1982; Yoneda, 1981). However, such an association may be more difficult to form and maintain, as little is known of these mixed-species groups, especially in terms of the cohesion of these associations (see Chapters 1 & 2), but it remains an intriguing proposal which could help to elucidate the costs and benefits of such groups.

Differential responses to aerial and terrestrial predation threats.

The current study demonstrated that *S. labiatus* are more alert for potential aerial predation threats than *S .fuscicollis* , but the work of Peres (1993b) suggests that *S. fuscicollis* may be more alert for terrestrial predators than their congeners. Therefore, it should be possible to demonstrate such complementary anti-predatory behaviour in captive tamarins. However, the height of most of the captive environments (<2m) may make it difficult to show this. It is probably more effective to test the behaviour of mixed-species groups in enclosures with more vertical height. For example, the "new enclosure" used in the current study (see Chapter 3) had a height of between 3.5m and 5m, allowing a better determination of whether or not either species were looking downwards. An examination of the exact direction of scanning could be undertaken, and other variables such as looking down towards fallen food items, could be excluded from the analysis. This procedure would allow for a better opportunity to demonstrate differences in anti-predatory strategy between the species. Such an experiment could be extended, from the examination of general vigilance, to the active monitoring of threats, where threatening stimuli could be placed at different heights in the environment, and the reaction of both species to threats could be recorded. This could take the form of using models of aerial predators (e.g. Moodie & Chamove, 1990; Price, 1990a; Brown *et al,* 1992), or presenting terrestrial predators in enclosed tanks (e.g Bayart & Anthouard, 1992). All these measures could be compared and contrasted between the species, and when in both monospecific and mixed-species groups.

Expansion of ecological validity.

S. labiatus and *S. fuscicollis* were demonstrated to behave in a manner which was essentially very similar to that of their counterparts in the wild. This was found in terms of the two species tolerating each other's presence with little or no direct interactions, with the *S. labiatus* being found to occupy a higher mean height in the enclosure, and also because the two species spent around 25% of their time within 1m of each other. These measures were carried out in a confined space, and any spatial and height differences may be attributed, at least partly, to this confinement. However, a mixed-species group which were allowed to free-range over a small wooden area, showed a high level of association between the species, even though the species had the potential to be 200m or more apart. There were no clear height differences, as the mean height used by each species varied on a daily basis, depending upon the use of resources within the area. Overall, it could be argued that this particular group formed an association that was broadly similar to those formed by their counterparts in the wild, and so increased the ecological validity to the study. On the other hand, due to the fact that this was the only mixed group to free-range, then it is difficult to argue that all captive groups would behave in a similar manner. Therefore, in order to extend the ecological validity of the present study, it would be reasonable to expand the free-ranging studies to include all captive mixed-species groups, so that the degree of association could be measured for all such groups. In addition, it may be prudent to conduct a long-term free-ranging study, of perhaps 6 months duration, in order to examine whether the degree of association changes over time.

7.8.2 Studies of wild tamarins.

Definition of association.

In order to show that two species form a mixed-species group, Waser (1980, 1982, 1984) has outlined some empirical formulae which determine whether or not an "association" actually exceeds the level of mere "chance" encounters. It is based on a theoretical situation where two groups are moving in a random manner, and predicts the amount of time the species should be found together, due solely to this random movement. This gives the most basic criteria with which to determine if an association takes place, and it would provide a starting point in the empirical examination of all tamarin associations. For example, it has not been shown that associations between *S. fuscicollis* and *Callithrix emiliae* occur for a time period that exceeds the time expected due to random movement. This could be one type of mixed-species group which may be tested with this formula.

Another parameter which is important in the study of tamarin mixed-species groups in the wild, is what distance do you use to determine whether two species are "in association". There is no universally accepted standard, and various researchers have used a variety of different measures, ranging from being "in close enough proximity to be observed as a single unit" (Pook & Pook, 1982 : 199), through to a distance of ≤ 20m (Heymann, 1990b; Terborgh, 1983). However, the 20m distance was derived from two different viewpoints; for Terborgh (1983) it was the limit of visibility in the habitat, while for Heymann (1990b) it applied to the radius of the average group spread. In his field study of *S. mystax* and *S. fuscicollis*, Peres (1991) has determined the mean group spread to be approximately 25m, and used this as an index of association. Finally, Buchanan-Smith (1989, 1990a) used a distance of ≤ 50m as her limit of association, as this was her quadrat size while radio-tracking poorly habituated groups of *S. labiatus* and *S. fuscicollis.* These measures are not exactly compatible, although they are all used to show a similar phenomenon. I suggest that there should be a standard criteria used to define what "association" means, in terms of the spatial distance between species, so that the results of all field studies can be directly comparable. I suggest this distance should be related to the radius of mean group spread for both species, so that association can be said to occur where individuals of both species are as close to each other, as the furthest "outlier" would be to the centre of their own group. In effect, this would probably be a distance of around 20 metres.

Lastly, I would suggest that future field studies should, where possible, rely on a set of commonly agreed measurements. This would be very important for estimations of group size and population density, as few studies make explicit the basis for the figures they present in the literature, and do not indicate whether they include infants or not. Such data are needed, if there is to be a systematic examination of tamarin behaviour and ecology, and would allow within-genera differences to be elucidated.

Learning & facilitation of responses in the wild.

As the "behavioural facilitation hypothesis" was found to be an important factor in the behaviour of captive tamarin mixed-species groups (see Chapter 5), it is essential to determine the extent and nature of such facilitation in a natural situation. This could be concerned with behaviour related to the location of food sources, or the reaction to potential threats. One relatively simple way of determining if behaviour is facilitated between the species, is to look at natural situations such as alarm call events. However, under field conditions it may not be easy to determine which individual was first to react to a potential threat, and also to show that the subsequent reaction of one species was due to the alarm calls, or the avoidance actions of their congeners (see Heymann, 1990c for a discussion of such problems). It may be possible to show that the alarm calls of one species are responded to by their congeners, during general observations, but a more fruitful approach might involve the use of the "playback paradigm" (Cheney & Seyfarth,1985; Seyfarth & Cheney, 1990). In this type of experiment, specific types of call are recorded in advance, and are played back under conditions which limit the interference of other variables, except the call itself. If each species were shown to react in an appropriate way to the call which is played back, in absence of the stimuli which elicited the call, then this would suggest that both species are able to transfer information about the presence of threatening stimuli to each other. If recorded calls are able to elicit responses outwith the presence of actual stimuli, then it is possible that such calls contain information which refer to the type of threat, and it may be appropriate to examine the reaction of each species to recordings of calls which have been given to both aerial and terrestrial predation threats, as such calls are known to be audibly distinct (e.g. Epple, 1975; Neyman, 1978). This is an interesting area for further investigation.

Responses related to the location of food are probably passed between the species by means of direct observation, but may also be passed through food directed calls (see Chapter 5). In the field, the most productive method for studying the facilitation of responses related to the presence of food between the species, may involve the systematic study of plant food use by mixed-species groups (e.g. Peres, 1991). However, it may be possible to conduct experiments with novel food items placed in different parts of the environment, and see which species is first to encounter such resources. If it can be manipulated successfully, then it may be possible to have situations where both species jointly encounter the resource, and provided that resource is of a large enough size, then it would be interesting to see if the other species can discover this resource due to the reactions of their congeners. Food could be in the form of items such as bananas, and the reactions of both species to the presence of traps (see Buchanan-Smith, 1989), suggests that the species may behave differently when faced with stimuli in different parts of their environment.

Vigilance and anti-predatory behaviour.

As group size has been demonstrated to be an important factor in the determination of the individual vigilance rate of captive tamarins (see Chapter 6), it is important to discover if a similar effect can be shown in wild tamarins. This could be done as part of long-term field studies, where the vigilance rate could be measured at different group sizes, and at different points in time, to see if changes in group composition directly affect the individual vigilance rate of that groups' members. A prediction to be examined would be that individuals in larger groups should have a lower mean vigilance rate per individual, than individuals in smaller sized groups. This could be tested for overall mixed-species group sizes, and for the group size of the two species separately.

Another area for testing, is the hypothesis that *S. fuscicollis* in *S. labiatus-S. fuscicollis* mixed-species groups may be more effective in the monitoring for terrestrial predation threats. This could be achieved through the observation of general vigilance patterns of both species in mixed-species groups, or though studies using interventional techniques. These could take the form of experiments similar to those of van Schaik & Mitrasetia (1990), who placed a snake model in a tree, testing its effects on wild long-tailed macaques (*Macaca fascicularis*). The presentation of such model snakes in the lower parts of the forest, and the subsequent reaction of both species to such models, may be help to confirm or deny any differences in response to predators. It is also possible to compare the reactions of each species to naturally occurring terrestrial threats such as tayras, coatis or felids.

Group sizes & ecology of monospecific and mixed-species groups of *S. fuscicollis* in Bolivia.

In Bolivia, *S. fuscicollis* is found to exist in monospecific groups and as part of mixed-species groups (see Chapter 1), although both types of grouping are not found in the same area. However, mixed-species groups are found in the Pando region of northern Bolivia, where their distribution is only as far south as Rio Tahuamanu, due to the lack of *S. labiatus* on the right bank of this river (e.g. Izawa & Bejarano, 1981; Rylands *et al.*, 1993). Single species groups of *S. fuscicollis* are found on the other side of this river, giving the possibility of studying both monospecific and mixed-species groups of *S. fuscicollis,* in ecological conditions which are probably very similar. This would allow an evaluation of parameters such a group size, diet, day range, and mean height use, in the two conditions. Specific predictions that could be tested might include ;

1) If the "predation hypothesis" is an important factor in controlling the group size of tamarins, then it is predicted that the group size of monospecific groups of *S. fuscicollis* will be larger than those participating in mixed-species groups.

2) If group size is constrained by other factors, such as breeding competition, then it is predicted that group size will not be significantly different in either condition.

3) If *S. fuscicollis* in mixed-species groups benefit from their congeners' knowledge of the position of large resources within their territory, then it is predicted that monospecific groups may have a more "haphazard" progression towards such large resources in their territory. The ability to locate large resources found high in the canopy may be related primarily to the vertical partitioning of the species, where members of the *S. mystax* group use a higher mean height of the forest. and may be presumed to have abetter knowledge of such areas.

Data could be collected to test such predictions, and other more general behavioural data could be collected, in order to determine whether the long-term survival of group members and infant survival rates differ between the conditions.

Comparative studies of *S. labiatus / S. imperator / S. mystax* associations.

Northern Bolivia may also provide an opportunity to examine the behaviour of the members of the *S. mystax* group, as all three species (*S. labiatus, S. mystax & S. imperator*) are reported to occur in the Pando region (Izawa & Bejarano, 1981). However, the actual distribution of these three species is very poorly understood (Rylands *et al.*, 1993), and it is not clear whether they are allopatric or sympatric, or whether their distributions are geographically separated by rivers or other physical barriers. This is an interesting idea which should be explored by a series of field observations, conducted at sites where each species are reported to occur ; in particular to discover where the local populations of each species begin and finish, and to see if there are behavioural or physical barriers between the species. It may be that the great similarities between the members of the *S. mystax* group (see Chapter 1), would prevent the association between members of this group, but this remains to be tested.

Another consequence of this distribution pattern, would be the opportunity to compare and contrast the behaviour and ecology of all three members of the *S. mystax* group, in terms how they utilise resources, the costs and benefits of forming mixed-species groups, and their general group size and ranging patterns. However, the fact that all three members of the *S. mystax* group are found in a relatively small area of Bolivia (see Rylands *et al.*, 1993), means that this gives an ideal opportunity to study these three species in an area which may be ecologically very similar for all three species. This would allow an evaluation of the similarities and differences between the species, which could control for, at least in part, any differences found due to only differences in habitat. Again, such a study would help to elucidate some of the costs and benefits involved in the formation of tamarin mixed-species associations, and would show whether or not the results of studies of any individual member of the *S. mystax* group could be generalised to apply to the other two species.

Associations between *S. fuscicollis* and *Callithrix emiliae*.

Since the discovery of sympatric populations of *S. fuscicollis* and *Callithrix emiliae*, in Rondonia (Martins *et al.*, 1987), where at least some of the groups were commonly found to form mixed-species groups (Ferrari & Lopes, 1992), such groups has been a potential source for comparative studies. These groups may not be as stable as *Saguinus-Saguinus* mixed-species groups, and there is probably not the same cohesive association, due to a greater degree of ecological similarity between the species, and the fact that both have a similar body weight (Ferrari & Martins, 1992), indicates there may be a higher degree of competition. Indeed, it has been suggested that *S. fuscicollis* may exploit the gum flow which *C.emiliae* are able to elicit by using their specialised dentition (Ferrari & Martins, 1992). This could be a possible benefit for the *S. fuscicollis* derived from being part of such an association, but only a systematic study will elucidate the details. However, reliance on such gum supplies during the dry season would be of great benefit to the *S. fuscicollis*, as due to the shortage of fruit, tamarins have to utilise alternative food sources, while marmosets are able to elicit a regular supply of gum through their bark-gouging (Ferrari & Lopes Ferrari, 1989). Such an ability would allow the *S. fuscicollis* to gain a degree of stability in resources, but the exact costs and benefits for both species are unclear. Only the careful measure of parameters such as the degree of association, ecological partitioning between the species, and the direction and nature of interactions between the species, would shed light on this association. In addition, this remains an interesting area of comparative study, as similarities and differences between the *Callithrix-Saguinus* and *Saguinus-Saguinus* associations may help to clarify the various costs and benefits of both types of association.

Territoriality

Terborgh (1983) originally suggested that both species in tamarin mixed-species groups perform a type of joint territoriality, where they jointly defend their resources from neighbouring mixed-species groups. The presumption was that a larger mixed-species group would be better at defending resources than smaller mixed-species groups. However, this is not necessarily the case, as Peres (1991) has detailed data which suggest that *S. mystax* are the main participants during encounters, when in mixed-species groups. Also, Garber (1988a) has presented data from which it may be surmised that the successful defence of a resource is dependent upon the number of *S. mystax* present. This position is further supported by the fact that both species in tamarin mixed-species groups do not defend territories from their congeners (e.g. Buchanan-Smith, 1991c; Garber, 1988a; Terborgh, 1983). Therefore, it may be more appropriate to describe it as parallel territoriality, where both species independently defend resources from their conspecifics, at the same time. If this is a more appropriate description of events, then it appears that it may not be the size of a mixed-species group per se, which is the critical factor in determining a successful defence of resources. This could be investigated in detailed long-term field studies, examining the competitive abilities of mixed-species troops containing different sized groups of each species, to determine whether it is the number of *S. fuscicollis*, the number of their congeners, or the size of the entire troop, which determines the successful defence of a resource. The testing could take the form of specific predictions such as ;

1) If members of the *S. mystax* group are responsible for determining a successful defence, then it is predicted that success should only be correlated to the number of individuals of these species, regardless of the size of *S. fuscicollis* groups.

2) If the defence is dependent upon the number of *S. fuscicollis*, then it is predicted that with all things being equal, the successful defence of resources by groups of their congeners should vary according to the number of *S. fuscicollis* present, where larger groups are presumably able to win in such circumstances.

3) If successful defence depends purely upon the mixed-species group size, then it is predicted that larger mixed-species groups should triumph over smaller groups in all encounters, regardless of the number of each species making up the overall size.

These predictions should be tested in a series of controlled experiments, where a whole range of different group sizes and group compositions are sampled for both species. This represents a real challenge, as tamarins may be very difficult to observe in the wild (see Chapter 2). Nevertheless, these studies would present a real test of whether or not joint territoriality occurs.

7.9 Final comment.

This study has outlined some of the potential costs and benefits of tamarin mixed-species groups, and has emphasised the importance of the "behavioural facilitation hypothesis", and its relevance to both the "predator avoidance hypothesis" and the "feeding efficiency hypothesis". The importance of the facilitation of behaviour may be related to the costs of such facilitation. This may be due to the fact that the type of advantages which can be passed between the species, usually have little or no cost to the species conducting the behaviour. This is because tamarin groups are probably based on a high degree of within-group cooperation (Caine, 1993), and behaviours related to parameters such as the position of food, or the presence of a threat, need to be passed on to other group members. Such an intraspecific facilitation may have benefits to the individuals' giving such a call, especially if they are related to the caller (Hamilton, 1964), and presumably must have benefits which outweigh any potential costs. If a call is directed towards a conspecific, then the fact that it may also alert a congener, may only be a cost to that species if the congener can take advantage of the situation. This may be the case when *S. fuscicollis* discover small, monopolisable resources, which their congeners can take advantage of, but would have little or no costs when applied to large resources or to alarm calls given in response to predation threats. This is related to the "behavioural differences hypothesis", as this suggests that behavioural differences between the two species may lead to the interspecific facilitation of behavioural responses.

Overall costs and benefits have been suggested for both species, but the main pattern which emerges, is that *S. labiatus* probably have relatively few costs, and many benefits from being in mixed-species groups, due to their exclusive dominance over the *S. fuscicollis.* However, the *S. fuscicollis* may have more costs due to their submissive position, but they may also have a greater range of benefits than their congeners, taking advantage of the large level of vigilance and vigorous territorial defence of the congeners. Nevertheless, more work is required if we are to fully understand all the costs and benefits involved in tamarin mixed-species groups.

References

Abordo, EJ. Mittermeier, RA., Lee, J. & Mason, P. (1975). Social grooming between squirrel monkeys and ukaris in a semi-natural environment. *Primates 16(2),* 217-221.

Abramson, M. (1979). Vigilance as a factor influencing flock formation among curlews, *Numenius arguata. Ibis 121*, 213-216.

Addington, RA., Caine, NG. & Schaffner, C. (1991). Factors affecting the food calls of red-bellied tamarins. *Am. J. Primatol 24* , 85 (Abstract).

Alexander, RD. (1974). The evolution of social behaviour. *Ann. Rev. Ecol. Syst. 5,* 325-383.

Allan, JR. (1986). The influence of species composition on behaviour in mixed-species cyprinid shoals. *J. of Fish Biology 29 (Supp.A),* 97-106.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour 49,* 227-267.

Ayres, JM. & Clutton-Brock, TH. (1992). River boundaries and species range in Amazonian primates. *The American Naturalist 140(3),* 531-537.

Baker, B. (1992). Guess who's coming to dinner ? *AAZPA 1992 Regional Proceedings,* 62-67.

Barnard, CJ. & Stephens, H. (1983). Costs and benefits of single and mixed-species flocking in fieldfares (*Turdus pilaris*) and redwings (*T. iliacus*). *Behaviour 84,* 91-123.

Barnard, CJ. & Thompson, DBA. (1985). *Gulls and plovers : the ecology and behaviour of mixed-species feeding groups.* Croom Helm, London.

Barnett, SA. & Cowan, PE. (1976). Activity, exploration, curiosity and fear : an ethological study. *Interdisciplinary Science Reviews 1(1),* 43-62.

Bartecki, U. & Heymann, EW. (1987). Field observation of snake-mobbing in a group of saddle-back tamarins, *Saguinus fuscicollis nigrifrons. Folia primatologica 48,* 199-202.

Bauers, K. & Snowdon, CT. (1990). Discrimination of chirp vocalizations in the cotton-top tamarin. *Am. J. Primatol. 21,* 53-60.

Bayart, F. & Anthouard, M. (1992). Responses to a live snake by *Lemur macaco macao* and *Lemur fulvus mayottensis* in captivity. *Folia primatologica 58,* 41-46.

Beck, BB. (1990). Managing zoo environments for reintroduction. *AAZPA 1991 Ann. Conf. Proc.* 436-440.

Beck, BB. Kleiman, DG., Castro, I., Rettberg-Beck, B. & Carvalho, C. (1990). Preparation of captive-born golden lion tamarins for release into the wild. In : *A case study in conservation biology : the golden lion tamarin.* (ed. DG Kleiman), Smithsonian Institution Press, Washington D.C.

Berger, J. (1978). Group size, foraging and antipredator ploys : an analysis of bighorn sheep decisions. *Behav. Ecol. Sociobiol. 4,* 91-99.

Berner, TO. & Grubb, TC. (1985). An experimental analysis of mixed-species flocking in birds of deciduous woodland. *Ecology 66(4),* 1229-1236.

Bernstein, IS. (1967). Intertaxa interactions in a Malayan primate community. *Folia primatologica 7,* 198-207.

Bernstein, IS. (1984). The adaptive value of maladaptive behaviour, or you've got to be stupid in order to be smart. *Ethology & Sociobiology 5* , 297-303.

Bertram, BC. (1978). Living in groups : predators and prey. In : *Behavioural Ecology : An evolutionary approach* (ed. JR Krebs, NB Davies), pp 64-96, Blackwell, Oxford.

Bertram, BC. (1980). Vigilance and group size in ostriches. *Animal Behaviour 28,* 278-286.

Beveridge, FM & Deag, JM. (1987). The effects of sex, temperature and companions, on looking up and feeding in single and mixed-species flocks of house sparrows (*Passer domesticus*), chaffinches (*Fringilla coelebs*), and starlings (*Sturnus vulgaris*). *Behaviour 100,* 303-320.

Boinski, S. (1989). Why don't *Saimiri oerstedii* and *Cebus capucinus* form mixed-species groups ?. *Int. J. Primatol. 10(2),* 102-114.

Bourliere, F., Hunkeler, C., & Bertrand, M. (1970). Ecology and behaviour of Lowe's guenon (*Cercopithecus campbelli lowei*) in the Ivory Coast. In: *Old world monkeys,* (ed. JR Napier & PH Napier), pp 297-350, Academic Press, New York.

Bowen, RA. (1982). The behaviour of three hand-reared lowland gorillas, (*Gorilla g. gorilla*) with emphasis on the response to a change in accommodation. *DODO; J. Jersey Wildl. Pres. Trust 17,* 63-69.

Box, HO. (1984). Behavioural responsiveness - experimental studies. In : *Primate Behaviour and social ecology.* (ed. HO Box), pp 147-179, Chapman & Hall, London.

Box, HO. (1988). Behavioural responses to environmental change. Observations on captive marmosets and tamarins (Callitrichidae). *Animal Technology 39(1),* 9-16.

Box, HO. (1991a). Training for life after release : simian primates as examples. *Symp. Zool. Soc. Lond. 62,* 111-123.

Box, HO. (1991b). Responsiveness to environmental change : interrelationships among parameters. In *Primate responses to environmental change* , pp 57-74, (ed. HO Box), Chapman & Hall, London.

Box, HO.(ed) (1991c). *Primate responses to environmental change*, Chapman & Hall, London.

Box, HO. & Morris, JM. (1979). Observing monkeys in northern Peru. *Social Biology & Human Affairs 44(2),* 134-142.

Box, HO. & Morris, JM. (1980). Behavioural observations on captive pairs of wild-caught tamarins (*Saguinus mystax*). *Primates 21,* 53-65.

Box, HO. & Pook, AG. (1974). A quantitative method for studying behaviour in small groups of monkeys in captivity. *Primates 15,* 101-105.

Bradbury, JW.(1975). Social organization and communication . In *Biology of Bats,* Vol 3 (ed. W Wimsatt), pp 1-72, Academic Press, New York.

Bronikowski, EJ., Beck, BB., & Power, M. (1989). Innovation, exhibition and conservation : free-ranging tamarins at the National Zoological Park. *AAZPA 1989 Ann. Conf. Proc.*

Brown, L. & Amadon, D. (1968). *Eagles, hawks and falcons of the world.* McGraw-Hill, New York.

Brown, MB., Kreiter, NA., Maple, JT. & Sinnott, JM. (1992). Silhouettes elicit alarm calls from captive vervet monkeys (*Cercopithecus aethiops*). *J. Comparative Psych. 106(4),* 350-359.

Buchanan, DB. Mittermeier, RA. van Roosmalen, MGM. (1981). The saki monkeys, genus *Pithecia,* In *Ecology and behaviour of Neotropical primates, vol. 1.* (ed. AF Coimbra-Filho & RA Mittermeier), Academia Brasileira de Ciencias, Rio de Janerio.

Buchanan-Smith, HM. (1989). *The Social Organisation and Mating Systems of the Red Bellied Tamarin (*Saguinus labiatus labiatus*): Behavioural Observations in Captivity and in the Field.* PhD thesis, University of Reading.

Buchanan-Smith, HM. (1990a). Polyspecific association of two tamarin species, *Saguinus labiatus* and *Saguinus fuscicollis,* in Bolivia. *Am. J. Primatol. 22,* 205-214.

Buchanan-Smith, HM. (1990b). Observations of Gray's bald face saki, *Pithecia i. irrorata,* in Bolivia. pp 2-8, in *Regional (U.K.) Studbook for the white-faced saki, Pithecia p pithecia,* 2.

Buchanan-Smith, HM. (1991a). A field study on the red-bellied tamarin, *Saguinus l. labiatus* in Bolivia. *Int. J. Primatol. 12,* 1-18.

Buchanan-Smith, HM. (1991b). Field observations of Goeldi's monkey, *Callimico goeldii,* in northern Bolivia. *Folia primatologica 145,* 1-4.

Buchanan-Smith, HM. (1991c). Encounters between neighbouring mixed-species groups of tamarins in northern Bolivia. *Primate Report 31,* 95-99.

Burger, J. & Gochfield, M. (1992). Effect of group size on vigilance while drinking in the coati, *Nasua narica* in Costa Rica. *Anim. Behav. 44,* 1053-1057.

Burger, J. & Gochfield, M. (1994). Vigilance in African mammals : differences among mothers, other females, and males. *Behaviour 131 (3-4),* 153-169.

Caine, NG. (1984). Visual scanning by tamarins. A description of the behavior and tests of two derived hypotheses. *Folia primatologica 43,* 59-67.

Caine, NG. (1986). Visual monitoring of threatening objects by captive tamarins (*Saguinus labiatus*). *Am. J. Primatol. 10,* 1-8.

Caine, NG. (1987). Vigilance, vocalizations, and cryptic behavior at retirement in captive groups of red-bellied tamarins (*Saguinus labiatus*). *Am. J. Primatol. 12,* 241-250.

Caine, NG. (1990). Unrecognised anti-predator behaviour can bias observational data. *Anim. Behav. 39,* 195-197.

Caine, NG. (1993). Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour : the role of predation pressure In : *Marmosets and tamarins. systematics, behaviour and ecology.,* (ed. AB Rylands), pp 200-219, Oxford University Press, Oxford.

Caine, NG. & Marra, SL. (1988). Vigilance and social organization in two species of primates. *Anim. Behav. 36,* 897-904.

Caine, NG. Potter, MP. Mayer, KE. (1992). Sleeping site selection by captive tamarins (*Saguinus labiatus*). *Ethology 90,* 63-71.

Caine, NG. & Weldon, PJ. (1989). Responses by red-bellied tamarins (*Saguinus labiatus*) to fecal scents of predatory and non-predatory Neotropical mammals. *Biotropica 21(2),* 186-189.

Caldwell, GS. (1981). Attraction to tropical mixed-species heron flocks : proximate mechanisms and consequences. *Behav. Ecol. Sociobiol. 8*, 9-103.

Cameron, R. Wiltshire, C. Foley, C. Dougherty, N. Aramayo, X. Rea, L. (1988). Bolivia '87 : an Oxford university conservation project. Final Report.

Cameron, R. & Buchanan-Smith, HM. (in press). Primates of the Pando, *Primate Conservation.*

Caraco, T.(1979). Time budgeting and group size : a test of theory.*Ecology 60,* 611-617.

Caraco, T.(1981). Risk-sensitivity and foraging groups.*Ecology 62,* 527-531.

Caraco, T. & Wolfe, (1975). Ecological determinants of group sizes of foraging lions.*Amer. Natur. 109,* 343-352.

Caraco, T., Martindale, S. & Pulliam, HR. (1980). Avian flocking in the presence of a predator. *Nature 285*, 400-401.

Cartmill, M. (1985). Climbing. In *Functional vertebrate morphology.* (ed. M Hildebrand, DM Bramble, KF Liem, DB Wake),pp 73-78, The Belknap press of Harvard University Press, Cambridge, Massachusetts.

Caro, TM., Roper, R., Young, M. & Dank, GR. (1979). Inter-observer reliability. *Behaviour 69,* 303-315.

Castro, R. & Soini, P. (1978). Field studies of *Saguinus mystax* and other callitrichids in Amazonian Peru. In *Biology and Conservation of the Callitrichidae,* (ed. DG Kleiman), pp 73-78, Smithsonian Institution Press, Washington D.C.

Chamove, AS. (1983). Role of dominance in macaque response to novel objects. *Motivation & Emotion 7(2),* 213-228.

Chamove, A. & Rohrhuber, B. (1989). Moving callitrichid monkeys from cages to outdoor areas. *Zoo Biology 8,* 151-163.

Chapman, CA., Wrangham, RW. & Chapman, LJ. (1995). Ecological constraints on group size : an analysis of spider monkey and chimpanzee subgroups. *Behav. Ecol. Sociobiol 36,* 59-70.

Charles-Dominique, P. (1977). *Ecology and behaviour of nocturnal primates.* Columbia University Press, New York.

Charnov, EL., Orians, GH. & Hyatt, K. (1976). Ecological implications of resource depression. *Am. Natur. 110,* 247-259.

Cheney, DL. & Seyfarth, RM. (1985). Vervet monkey alarm calls : manipulation through shared information ?. *Behaviour 94,* 150-166.

Cheney, DL & Wrangham, RW. (1987). Predation. In: *Primate Societies,* (ed. BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, TT Struhsaker), pp 227-239, University of Chicago press, London.

Chilton, G. & Sealey, SG. (1987). Species roles in mixed-species feeding flocks of seabirds. *J. of Field Ornithology 58(4),* 456-463.

Christen, A. & Geissmann, T. (1994). A primate survey in northern Bolivia, with special reference to Goeldi's monkey, *Callimico goeldii. Int. J. Primatol. 15(2),* 239-273.

Clark, AB. (1991). Individual variation in responsiveness to environmental change. In *Primate responses to environmental change* , (ed. HO Box), pp 91-110, Chapman & Hall, London.

Clark, CW. & Mangel, M. (1986). The evolutionary advantages of group foraging. *Theor. Popul. Biol 30,* 45-75.

Clarke, AS. Juno, CJ. & Maple, TL. (1982). Behavioural effects of a change in the physical environment : a pilot study of captive chimpanzees. *Zoo Biology 1,* 371-380.

Clarke, AS. & Lindberg, DG. (1993). Behavioural contrasts between male cynomolgus and lion-tailed macaques. *Amer. J. Primatol. 29,* 49-59.

Cleveland, J. & Snowdon, CT. (1982). The complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). *Z. Tierpsychol. 58,* 231-270.

Cleveland, J. & Snowdon, CT. (1984). Social development during the first twenty weeks in the cotton-top tamarin (*Saguinus o. oedipus*). *Anim. Behav. 32,* 432-444.

Clutton-Brock, TH. & Harvey, PH (1977). Primate ecology and social organization. *J. Zool. Lond. 183,* 1-39.

Coates, A. & Poole, TB. (1983). The behavior of the callitrichid monkey, *Saguinus labiatus,* in the laboratory. *Int. J. Primatol. 4,* 339-371.

Cody, ML. (1971). Finch flocks in the Mojave Desert. *Theor. Pop. Biol. 2,* 142-148.

Coimbra-Filho, AF. & Mittermeier, RA. (1977). Conservation of the Brazilian lion tamarins (*Leontopithecus rosalia*). In *Primate Conservation.* (ed. Prince Ranier III of Monaco & GH Bourne), pp 59-84, Academic Press, New York.

Coimbra-Filho, AF. (1978). Natural shelters of *Leontopithecus rosalia* and some ecological implications (*Callitrichidae : Primates*). In *Biology and conservation of the Callitrichidae,* (ed. DG Kleiman), pp 79-89, Smithsonian Institution Press, Washington D.C.

Coolican, H. (1990). *Research methods and statistics in psychology.* Hodder & Stoughton, London.

Cords, M. (1987). Mixed-species association of *Cercopithecus* monkeys in the Kakamega forest, Kenya. *University of California Publ. Zoology Vol. 117.* 1-109.

Cords, M. (1990a). Vigilance and mixed-species association of some east African forest monkeys. *Behav. Ecol. Sociobiol. 26,* 297-300.

Cords, M. (1990b). Mixed-species association of east African guenons ; general patterns or specific examples ?. *Am. J. Primatol. 21,* 101-114.

Crandlemire-Sacco, J. (1988). An ecological comparison of 2 sympatric primates : *Saguinus fuscicollis* and *Callicebus moloch* of Amazonian Peru. *Primates 29(4),* 465-475.

Curio, E. (1976). *The ethology of predation.* Springer-Verlag, Berlin.

Daly, M. & Wilson, M. (1983). *Sex, evolution and behaviour., 2nd Edition,* Willard Grant Press, Boston.

Dawson, GA. (1976). *Behavioral Ecology of the Panamanian Tamarin,* Saguinus oedipus (Callitrichidae, Primates). PhD thesis, Michigan State University. University Microfilms International, Ann Arbor, Michigan.

Dawson, GA. (1978). Composition and stability of social groups of the tamarin, *Saguinus oedipus geoffroyi,* in Panama: ecological and behavioral implications. In: *Biology and Conservation of the Callitrichidae,* (ed. DG KLEIMAN), pp 23-37. Smithsonian Institution Press, Washington D.C.

Dawson, GA. (1979). The use of time and space by the Panamanian tamarin, *Saguinus oedipus. Folia primatologica 31,* 253-284.

Dawson, GA. & Dukelow, WR. (1976). Reproductive characteristics of free-ranging Panamanian tamarins (*Saguinus oedipus geoffroyi*). *J. Med. Primatol. 5,* 266-275.

Debrot, AO. & Myreburg, AA. (1988). Intraspecific avoidance as a proximate cause for mixed-species shoaling by juveniles of a western Atlantic surgeonfish. *Bulletin of Marine Science 43(1),* 104-106.

Demaria, C & Thierry, B. (1988). Responses to animal stimulus photographs in stumptailed macaques (*Macaca arctoides*). *Primates 29(2),* 237-244.

Diamond, JM. (1981). Mixed species foraging groups. *Nature 292,* 408-409.

Dolins, FL. (1993). *Spatial relational learning and foraging in cotton-top tamarins.* Unpublished PhD thesis, University of Stirling, U.K.

Dolins, FL. & Garber, PA. (1994). The use of spatial and perceptual cues in foraging by captive cotton-top tamarins (*Saguinus o. oedipus*) and wild moustached tamarins (*Saguinus mystax*). *Primate Eye 52,* 26 (Abstract).

Dunbar, RIM. (1976). Some aspects of research design and their implications in the observational study of behaviour. *Behaviour 58,* 78-98.

Dunbar, RIM. (1988). *Primate Social Systems.* Croom Helm, London.

Eguchi, K., Yamagishi, S. & Randriansolo, V. (1993). The composition and foraging behaviour of mixed-species flocks of forest living birds in Madagascar. *Ibis 135(1),* 91-96.

Ekman, J. (1987). Exposure and time use in willow tit flocks : the cost of subordination. *Animal Behaviour 35,* 445-452.

Ekman, J. & Hake, M. (1988). Avian flocking reduces starvation risk : an experimental demonstration. *Behav. Ecol. Sociobiol. 22,* 91-94.

Elder, WH. & Elder, NL. (1970). Social groupings and primate associations of the bushbuck (*Tragelaphus scriptus*). *Mammalia 34,* 356-362.

Elgar, MA. (1989). Predator avoidance and group size in mammals and birds : a critical review of the empirical evidence. *Biological Review 64,* 13-33.

Elowson, AM., Tannenbaum, PL. & Snowdon, CT. (1991). Food associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour 42,* 931-937.

Emmons, LH. (1987). Comparative feeding ecology of felid in a Neotropical rainforest. *Behav. Ecol. Sociobiol. 20,* 271-283.

Emmons, LH. & Feer, F. (1990). *Neotropical rainforest mammals : a field guide.* University of Chicago Press, London.

Encarnacion, F.(1990). Informe 01/90 Sub-proyecto : Investigacion y manejo de *Saguinus labiatus* en el sur oriente del Peru. Unpublished report, Proyecto Peruano de Primatoligia "Manuel Moro Sommo', Iquitos.

Encarnacion, F. & Castro, R. (1978). Informe preliminar sobre censo de primatas no humanos en el sur-oriente peruano : Iberia e Inapart (Departamento de Madre de Dios), Mayo 15-Junio 14, 1978. Unpublished report, Proyecto Peruano de Primatologica, Iquitos.

Encarnacion, F., Moya, IL., Soini, P., Tapia, J., & Aquino, R. (1978). La captura de Callitrichidae (*Saguinus y Cebuella*) en la Amazonia Peruana. In : *Boletin del comite regional de coordinacion del proyecto primates ; Publ. por el com. reg. coord. proy. primates, Vol 1, No1, Octubre 1978.*

Epple, G. (1975). Parental behavior in *Saguinus fuscicollis ssp.* (Callitrichidae). *Folia primatologica 24,* 221-238.

Epple, G. (1981). Effects of pre-pubertal castration on the development of the scent glands, scent marking and aggression in the saddle back tamarin (*Saguinus fuscicollis, Callitrichidae, Primates*), *Hormones & Behavior 15(1),* 54-67.

Epple, G. (1982). Effects of pre-pubertal ovariectomy on the development of the scent glands, scent marking and aggressive behaviors of female tamarin monkeys (*Saguinus fuscicollis*), *Hormones & Behavior 16(3),* 330-342.

Epple, G. & Katz, Y. (1980). Social influences on first reproductive success and related behaviors in the saddle-back tamarin (*Saguinus fuscicollis*). *Int. J. Primatol. 1,* 171-183.

Epple, G. & Katz, Y. (1984). Social influences on estrogen excretion and ovarian cyclicity in saddle back tamarins (*Saguinus fuscicollis*). *Am. J. Primatol. 6,* 215-227.

Eudey, AA. (1980). Pleistocene glacial phenomena and the evolution of Asian macaques. In *The macaques : studies in ecology, behavior and evolution.* (ed. DG Lindburg), pp 52-83, Van Nostrand-Reinhold, New York.

Fairbanks, LA. (1993). Risk taking by juvenile vervet monkeys. *Behaviour 124 (1-2),* 57-72.

Fairbanks, LA. & McGuire, MT. (1993). Maternal protectiveness and response to the unfamiliar in vervet monkeys. *Am. J. Primatol. 30,* 119-129.

FAO *Soil Map of the World.* 1971.

Feistner, ATC. (1985). *Food-sharing in the Cotton-top Tamarin (*Saguinus oedipus oedipus). MSc thesis, University of Stirling.

Feistner, ATC. & Chamove, AC. (1986). High motivation toward food increases food-sharing in cotton-top tamarins. *Dev. Psychobiol. 19,* 439-452.

Feistner, ATC. & McGrew, WC. (1989). Food sharing in primates : a critical review. In : *Perspectives in primate biology, Vol 3.* (ed. PK Seth & S. Seth), pp 21-36, Todays & Tomorrows Printers & Publishers, New Delhi.

Feistner, ATC. & Price, EC. (1990). Food-sharing in cotton-top tamarins (*Saguinus oedipus*). *Folia primatologica 54,* 34-45.

Ferrari, SF. (1993). Ecological differentiation in the Callitrichidae. In : *Marmosets and tamarins. systematics, behaviour and ecology.,* (ed. AB Rylands), pp 314-328, Oxford University Press, Oxford.

Ferrari, SF. & Lopes-Ferrari, MA. (1989). A re-evaluation of the social organisation of the Callitrichidae, with reference to the ecological differences between genera. *Folia primatologica. 52,* 132-147.

Ferrari, SF. & Lopes-Ferrari, MA. (1992). New data on the distribution of primates in the region of the confluence of the Jiparana and Madeira Amazonas and Rondonia, Brazil. *Goeldiana Zoologia, Numero 11: 31 de janeiro de 1992.*

Ferrari, SF. & Martins, ES. (1992). Gummivory and gut morphology in two sympatric callitrichids (*Callithrix emiliae* and *Saguinus fuscicollis weddelli*) from western Brazilian Amazonia. *Am. J. Phys. Anthro. 88,* 97-103.

Ferrari, SF. & Rylands, AB. (1994). Activity budgets and differential visibility in field studies of three marmosets (*Callithrix spp.*). *Folia primatologica 63,* 78-83.

Fitzgibbon, CD. (1990). Mixed species grouping in Thomson's & Grant's gazelles : the antipredator benefits. *Animal Behaviour 39,* 1116-1126.

Fitzgibbon, CD. (1990). The costs and benefits of predator inspection behaviour in Thompson's gazelles. *Behav. Ecol. Sociobiol. 34,* 139-148.

Fleagle, JG. & Mittermeier, RA. (1980). Locomotor behavior, body size and comparative ecology of seven Suriname monkeys. *Am. J. Phys. Anthro. 52,* 301-314.

Ford, SM. (1980). Callitrichids as phyletic dwarfs, and the place of Callitrichidae in Platyrrhini. *Primates 21,* 31-43.

Fragaszy, DM. (1979). Titi and squirrel monkeys in a novel environment. In *Captivity and behaviour : primates in breeding colonies, laboratories and zoos.*, (ed. J Erwin, TL Maple, G Mitchel), pp 172-216, van Nostrand Reinhold, New York.

Fragaszy, DM & Mason, WA. (1978). Response to novelty in *Saimiri* and *Callicebus* : influence of social context. *Primates 19(2),* 311-331.

Freese, CH., Freese, MA. & Castro, RN. (1978). The status of callitrichids in Peru. In : *Biology and Conservation of the Callitrichidae*, (ed. DG Kleiman), pp 121-130,Smithsonian Institution Press, Washington D.C.

Freese, CH., Heltne, PG., Castro, RN & Whitesides, G. (1982). Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. *Int. J. Primatol. 3,* 53-90.

French, JA. (1983). Lactation and fertility: an examination of nursing and inter-birth intervals in cotton-top tamarins (*Saguinus o. oedipus*). *Folia primatologica 40,* 276-282.

French, JA., Abbott, DH. Scheffler, G, Robinson, JA & Goyt, RW (1983). Cyclic excretion of urinary oestrogens in female tamarins (*Saguinus oedipus*). *J. Reprod. Fert. 67,* 177-184.

French, JA., Abbott, DH. & Snowdon, CT. (1984). The effect of social environment on estrogen excretion, scent marking, and sociosexual behaviour in tamarins (*Saguinus oedipus*). *Am. J. Primatol. 6,* 155-167.

French, JA. & Cleveland J. (1984). Scent-marking in the tamarin, *Saguinus oedipus*: sex differences and ontogeny. *Anim. Behav. 32,* 615-623.

French, JA. & Snowdon, CT. (1981). Sexual dimorphism in response to unfamiliar intruders in the tamarin, *Saguinus oedipus. Anim. Behav. 29,* 822-829.

French, JA. & Inglett, B. (1991). Responses to novel social stimuli on callitrichid monkeys. In *Primate responses to environmental change* , (ed. HO Box), pp 275-294, Chapman & Hall, London.

Galef, BG., Mittermeier, RA. & Bailey, RC. (1976). Predation by tayra (*Eira barbara*). *J. Mammal. 54,* 152-154.

Garber, PA. (1980a). Locomotor behavior and feeding ecology of the Panamanian tamarin (*Saguinus oedipus geoffroyi,*), Callitrichidae, Primates. PhD Thesis, Washington University, St Louis.

Garber, PA. (1980b). Locomotor behavior and feeding ecology of the Panamanian tamarin (*Saguinus oedipus geoffroyi,* Callitrichidae, Primates). *Int. J. Primatol. 1,* 185-201.

Garber, PA.(1984a). Proposed nutritional importance of plant exudates in the diet of the Panamanian tamarin, *Saguinus oedipus geoffroyi. Int. J. Primatol. 5,* 1-15.

Garber, PA. (1984b). Use of habitat and positional behaviour in a Neotropical primate, *Saguinus oedipus.* In : *Adaptations for foraging in non-human primates,* (eds. PS Rodman & JHG Cant), pp 112-133, Columbia University Press, New York.

Garber, PA. (1986). The ecology of seed dispersal in 2 species of callitrichid primates (*Saguinus mystax & Saguinus fuscicollis*).*Am. J. Primatol. 10,* 155-170.

Garber, PA. (1987). Foraging strategies among living primates. *Ann Rev. Anthro. 16,* 339-364.

Garber, PA. (1988a). Diet, foraging patterns and resource defence in a mixed-species troop of *Saguinus mystax* and *Saguinus fuscicollis,* in Amazonian Peru. *Behaviour 105,* 18-34.

Garber, PA. (1988b). Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis,* Callitrichidae, Primates) in Amazonian Peru. *Biotropica 20,* 100-106.

Garber, PA. (1989). Role of spatial memory in primate foraging patterns : *Saguinus mystax* and *Saguinus fuscicollis, Am. J. Primatol. 19,* 203-216.

Garber, PA. (1991). A comparative study of positional behaviour in 3 species of tamarin monkeys. *Primates 32(2),* 219-230.

Garber, PA. (1992). Vertical clinging, small body size and the evolution of feeding adaptations in the Callitrichidae. *Am. J. Phys. Anthro. 88,* 469-482.

Garber, PA. (1993a). Seasonal patterns of diet and ranging in 2 species of tamarin monkeys ; stability versus variability. *Int. J. Primatol. 14,* 145-166.

Garber, PA. (1993b). Feeding ecology and behaviour of the genus *Saguinus.* In : *Marmosets and tamarins. systematics, behaviour and ecology.,* (ed. AB Rylands), pp 273-295, Oxford University Press, Oxford.

Garber, PA. (1994). Phylogenetic approach to the study of tamarin and marmoset social systems. *Am. J. Primatol. 34,* 199-219.

Garber, PA., Moya, L. & Malaga, C. (1984). A preliminary field study of the moustached tamarin monkey (*Saguinus mystax*) in northeastern Peru: questions concerned with the evolution of a communal breeding system. *Folia primatologica. 42,* 17-32.

Garber, PA, Pruetz, JD. & Isaacson, J. (1993a). Patterns of range use, range defense, and intertroop spacing in moustached tamarin monkeys (*Saguinus mystax*). *Primates 34(1),* 11-25.

Garber, PA., Encarnacion, F., Moya, L. & Pruetz, JD. (1993b). Demographic and reproductive patterns in moustached tamarin monkeys (*Saguinus mystax*) : implications for reconstructing Platyrrhine mating systems. *Am. J. Primatol. 29,* 235-254.

Garber, PA., Bolen, RH. & Evans, S. (1993c). the use of color, odor and spatial cues in primate decision-making. *Am. J. Primatol. 30,* 312 (Abstract).

Garber, PA. & Hannon, B. (1993). Modelling monkeys : a comparison of computer-generated and naturally occurring foraging patterns in 2 species of Neotropical primates. *Int. J. Primatol. 14(6),* 827-854.

Garber, PA. & Kinzey, WG. (1992). Feeding adaptations in New world primates : an evolutionary perspective : Introduction. *Am. J. Phys. Anthro. 88,* 411-413.

Garber, PA. & Sussman, RW. (1984). Ecological distinctions between sympatric species of *Saguinus & Sciureus. Am. J. Phys. Anthro. 65,* 135-146.

Garber, PA. & Teaford, MF (1986). Body weights in mixed species troops of *Saguinus mystax mystax* and *Saguinus fuscicollis nigrifrons* in Amazonian Peru. *Am. J. Phys. Anthropol. 71,* 331-336.

Garcia, JE. & Cases, V. (1989). El estado de la primatologia en Bolivia. *Bol. Primatol. Lat. 1(1),* 21-35.

Gartlan, JS. & Struhsaker, TT. (1972). Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, west Africa. *J. Zool. Lond. 168,* 221-266.

Gautier-Hion, A. (1988). Polyspecific associations among forest guenons : ecological, behavioural and evolutionary aspects. In : *Primate radiation : evolutionary biology of the African guenons.* (ed. A Gautier-Hion, F. Bourliere, JP Gautier & K Kingdon), pp 452-476. Cambridge University Press, Cambridge

Gautier-Hion, A. & Gautier, JP. (1974). Les associations polyspecifiques de Cercopitheques de plateau de M'passa (Gabon). *Folia primatologica 22,* 134-177.

Gautier-Hion, A., Quris, R. & Gautier, JP. (1983). Monospecific vs. polyspecific life: a comparative study of foraging and antipredatory tactics in a community of Cercopithecus. *Behav. Ecol. Sociobiol. 12,* 325-335.

Gautier-Hion, A. & Tutin, CEG.(1983). Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Folia primatologica 51,* 149-151.

Glander, KE., Tapia, J. & Fachin, A. (1984). The impact of cropping on wild populations of *Saguinus mystax* and *Saguinus fuscicollis* in Peru. *Am. J. Primatol. 7,* 89-97.

Glickman, SE. & Sroges, RW. (1966). Curiosity in zoo animals. *Behaviour 26*, 151-188.

Godin, JGJ. (1986). Antipredator function of shoaling in teleost fishes : a selective review. *Naturaliste Canadienne (Revue Ecologie Systeme) 113*, 241-250.

Goldizen, AW. (1987a). Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behav. Ecol. Sociobiol. 20*, 99-109.

Goldizen, AW. (1987b). Tamarins and marmosets: communal care of offspring. In *Primate Societies*, (ed. BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, & TT Struhsaker), pp 34-43, University of Chicago Press, London.

Goldizen, AW. (1988). Tamarin and marmoset mating systems: unusual flexibility. *Trends Ecol. Evol. 3,* 36-40.

Goldizen, AW. (1989). Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). *Behav. Ecol. Sociobiol. 24,* 79-89.

Goldizen, AW. (1990). A comparative perspective on the evolution of tamarin and marmoset social systems. *Int. J. Primatol. 11(1)*, 63-83

Goldizen, AW. & Terborgh, J. (1986). Cooperative polyandry and helping behavior in saddle-backed tamarins (*Saguinus fuscicollis*). In : *Primate Ecology and Conservation*, (ed. J. Else & P. Lee), pp 191-198, Cambridge University Press, London.

Goldizen, AW. & Terborgh, J. (1989). Demography and dispersal patterns of a tamarin population: possible causes of delayed breeding. *Am. Nat. 134,* 208-224.

Goldizen, AW., Terborgh, J., Cornejo, F., Porras, DT. & Evans, R. (1988). Seasonal food shortage, weight loss, and the timing of births in saddle-back tamarins (*Saguinus fuscicollis*). *J. Anim. Ecol. 57*, 893-901.

Gosling, LM. (1980). Defence guilds of savannah ungulates as a context for scent communication. *Symp. Zool. Soc. Lond. 45*, 195-212.

Goss-Custard, JD. (1970). Feeding dispersion in some overwintering birds, In *Social behavior in birds and mammals*, (ed. JH Crook), pp 3-36, Academic Press, New York.

Goss-Custard, JD. (1976). Variation in the dispersion of redshank *Tringa totanus* on their winter feeding grounds. *Ibis 118*, 257-263.

Gower, EC. (1990). The long-term retention of events in monkey memory. *Behav. Brain Res. 38(3)*, 191-198.

Graves, GR. & Gotelli, NJ. (1993). Assembly of avian mixed-species flocks in Amazonia. *Proc. Nat. Acad. Sci. U.S.A. 90(4)*, 1388-1391.

Greene, J. & D'Oliveira, M. (1982). *Learning to use statistical tests in psychology.* Open University Press, Milton Keynes.

Greene, SE., Nealis, PM. & Suomi, SJ. (1977). Novelty and familiarity in discrimination learning by rhesus monkeys. *Bul. of the Psychonomic Soc. 10(5)*, 399-401.

Groom, MJ. (1992). Sand colored nighthawks parasitize the antipredator behavior of three nesting bird species. *Ecology 73(3),* 785-793.

Hamilton,WD. (1964). The genetical evolution of social behaviour. I, II. *J. Theor. Biol. 7,* 1-52.

Hamilton,WD. (1971).Geometry of the selfish herd. *J. Theor. Biol. 31,* 295-311.

Hardie SM., Day RT., Buchanan-Smith HM. (1993). Mixed-species *Saguinus* groups at Belfast Zoological Gardens. *Neotropical Primates 1(4),* 19-21.

Haverschmidt, F. (1968). *Birds of Surinam.* Oliver & Boyd, Edinburgh.

Hayashi, K. (1975). Interspecific interaction of primate groups in Kibale forest, Uganda. *Primates 16,* 269-283.

Hayes, SL. & Snowdon, CT. (1990). Predator recognition in cotton-top tamarins (*Saguinus oedipus*). *Am. J. Primatol. 20,* 283-291.

Heatwole, H. (1965). Some aspects of the association of cattle egrets with cattle. *Anim. Behav. 13,* 79-83.

Hernandez-Camancho, J. & Cooper, RW. (1976). The nonhuman primates of Colombia. In *Neotropical Primates. Field Studies and Conservation,.*(eds. RW Thorington, Jr & PG Heltne), pp 35-69, National Academy of Sciences, Washington DC.

Hershkovitz, P. (1977). *Living New World Monkeys (Platyrrhini).* University of Chicago Press, Chicago.

Heymann, EW. (1987). A field observation of predation on a moustached tamarin (*Saguinus mystax*) by an anaconda. *Int. J. Primatol. 8,* 193-195.

Heymann, EW. (1990a). Social behaviour and infant carrying in a group of moustached tamarins, *Saguinus mystax (Primates : Platyrrhini : Callitrichidae). Primates 31(2),* 193-196.

Heymann, EW. (1990b). Interspecific relations in a mixed-species troop of moustached tamarins *Saguinus mystax* and saddle-back tamarins *Saguinus fuscicollis (Primates : Platyrrhini : Callitrichidae*), at the Rio Blanco, Peruvian Amazonia. *Am. J. Primatol. 21,* 115-127.

Heymann. EW. (1990c). Reactions of wild tamarins, *Saguinus mystax & Saguinus fuscicollis* to avian predators. *Int. J. Primatol. 11(4),* 327-337.

Heymann, EW. (in press). Social behavior of wild moustached tamarins, *Saguinus mystax,* at the Estacion Biologica Quebrada Blanco, Peruvian Amazonia. *Am. J. Primatol.*

Heymann, EW. & Sicchar Valdez, LA. (1988). Interspecific social grooming in a mixed troop of tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Platyrrhini : Callitrichidae), in an outdoor enclosure. *Folia primatologica 50,* 221-225.

Hinde, RA. (1973). On the design of check-sheets. *Primates 14,* 393-406.

Hodge, MA & Uetz, GW. (1992). Antipredator benefits of single-species and mixed-species grouping by *Nephila clavipes* (L),(Araneae, Tetragnathidae). *J. Arachnology 209(3),* 212-216 (Abstract).

Hoogland, JL. & Sherman, PW. (1976). Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol. Monogr. 46,* 33-58.

Hubrect, RC. (1984). Field observations on group size and composition of the common marmoset (*Callithrix jacchus jacchus*), at Tapacura, Brazil. *Primates 25,* 13-21.

Izawa, K. (1975). Foods and feeding behaviour of monkeys in the upper Amazon. *Primates 16,* 295-316.

Izawa, K. (1976). Group sizes and compositions of monkeys in the upper Amazon basin. *Primates 17,* 367-399.

Izawa, K. (1978). A field study of the ecology and behavior of the black-mantle tamarin (*Saguinus nigricollis*). *Primates 19,* 241-274.

Izawa, K. (1979). Foods and feeding behaviour of wild black-capped capuchin (*Cebus apella*). *Primates 21,* 57-76.

Izawa, K. & Bejarano, G. (1981). Distribution ranges and patterns of non-human primates in western Pando, Bolivia. *Kyoto Univ. Overseas Reports of New World Monkeys 2,* 1-12.

Izawa, K. & Yoneda, M. (1981). Habitat utilization of nonhuman primates in a forest of western Pando. *Kyoto Univ. Overseas Reports of New World Monkeys 2,* 13-22.

Jacobsen, OW. & Ugelvik, M. (1994). Effects of presence of waders on grazing and vigilance behaviour in breeding widgeon, *Anas penelope. Anim. Behav. 47,* 488-490.

Jaenicke, C. & Ehrlich, A. (1972). Effects of animate vs inanimate stimuli on curiosity behaviour in greater galago and slow loris. *Primates 23,* 95-104.

Janson, CH. & van Schaik, CP. (1988). Recognising the many faces of primate food competition : methods. *Behaviour 105(1-2),* 165-186.

Janson, CH. Terborgh, J. Emmons, LH. (1981). Non-flying mammals as polinating agents in the Amazonian forest. *Biotropica,* suppl. 1-6.

Johnson, WE. & Balph, DF. (1990). Resource acquisition in the presence of novelty by coyotes of different rank. *J. Wildl. Manage. 54(4),* 582-586.

Jolly, A.(1964). Prosimians' manipulation of simple object problems. *Anim. Behav. 12,* 560-572.

Jolly, A. (1966). *Lemur behavior.* University of Chicago Press, Chicago.

Jones, RB. & Andrew, RK. (1992). Responses of adult domestic cocks and capons to novelty and alarming stimuli. *Behav. Processes 26(2-3),* 189-200.

Joubert, A. & Vauclair, J. (1986). Reaction to novel objects in a troop of guinea baboons : approach and manipulation. *Behaviour 96(1-2),* 92-104.

Kenward, RE. (1978). Hawks and doves : attack success and selection in goshawk flights at wood-pigeons. *J. Anim. Ecol. 47,* 449-460.

Kinzey, WG. (1981). The titi monkeys, genus *Callicebus.* In *Ecology and behavior of Neotropical primates.* (ed. AF Coimbra-Filho & RA Mittermeier), pp 241-276. Academia Brasileira de Ciencias, Rio de Janeiro.

Kinzey, WG. (1986). New World primate field studies: what's in it for anthropology ? *Ann. Rev. Anthropol. 15,* 121-148.

Kinzey, WG. & Norconk, MA. (1990). Hardness as a basis of fruit choice in 2 sympatric primates. *Am. J. Phys. Anthro. 81,* 5-15.

Klein, BC. (1988). Weather dependent mixed-species flocking during the winter. *Auk 105(3),* 583-584.

Klein, LL & Klein, DJ. (1973). Observations of two types of Neotropical primate intertaxa associations. *Am. J. Phys. Anthro. 38,* 649-654.

Klein, LL. & Klein, DJ. (1977). Feeding behaviour of the Colombian spider monkey. In *Primate ecology,* (ed. TH Clutton-Brock), pp 153-181, Academic Press, New York.

Kohlhaas, AK. (1991). Primate populations in northern Bolivia. *Primate Conservation 9,* 93-97.

Krebs, JR. (1973). Social learning and the significance of mixed species flocks of chickadees (*Parus spp.*). *Can. J. Zool. 51,* 1275-1288.

Krebs, JR. (1974). Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). *Behaviour 51,* 99-134.

Krebs, JR. & Davies, NB. (1981). *An introduction to behavioural ecology.* Blackwell Scientific Publications, Oxford.

Krebs, JR. & Davies, NB. (1987). *An introduction to behavioural ecology, 2nd edition.* Blackwell Scientific Publications, Oxford.

Krebs, JR., MacRoberts, MH. & Cullen, JM. (1972). Flocking and feeding in the great tit *Parus major* - an experimental study. *Ibis 114,* 507-530.

Kruuk, H. (1964). Predators and antipredator behaviour of the black-headed gull, *Larus ridibundus. Behaviour suppl. 11,* 1-129.

Lagory, KE. (1986). Habitat, group size and the behaviour of white-tailed deer. *Behaviour 98,* 168-179.

Landeau, L. & Terborgh, J. (1986). Oddity and the "confusion effect" in predation. *Anim. Behav. 34,* 1372-1380.

Lawrence, AB., Terlouw, EMC. & Illius, AW. (1991). Individual differences in behavioural responses of pigs exposed to non-social and social challenges. *Appl. Anim. Behav. Sci. 30(1-2),* 73-76.

Lazarus, J. (1979). Flock size and behaviour in captive red-billed weaverbirds (*Quela quela*) : implications for social facilitation and the functions of foraging. *Behaviour 71,* 127-145.

Lea, SEG. (1984). *Instinct environment and behaviour..* Methuen, London.

Lendrem, DW. (1984). Flocking, feeding and predation risk: absolute and instantaneous feeding rates. *Anim. Behav. 32,* 298-299.

Leutenegger, W. (1973). Maternal-fetal weight relationships in primates. *Folia primatologica 20,* 280-293.

Leutenegger, W.(1980). Monogamy in callitrichids: a consequence of phyletic dwarfism? *Int. J. Primatol. 1,* 95-98.

Lima, SL (1990). The influence of models on the interpretation of vigilance. In : *Interpretation and explanation in the study of animal behavior, Vol 2. Explanation, evolution and adaptation.*, (ed. M. Bekoff & D. Jamieson), pp 246-267, Westview Press, Boulder, Colorado.

Lima, SL (1995). Back to basics of antipredatory vigilance : the group size effect. *Anim. Behav. 49,* 11-20.

Lindsay, NBD. (1980). A report on a field study of Geoffroy's tamarin, *Saguinus geoffroyi. Dodo, J. Jersey Wildl. Preserv. Trust 17,* 27-51.

Lipetz, VE & Bekoff, M. (1982). Group size and vigilance in pronghorns. *Z. Tierpsychol. 58,* 203-216.

MacKenzie, MM. McGrew, WC. & Chamove, AS. (1985). Social preferences in stump-tailed macaques (*Macaca arctoides*) : effects of companionship,kinship and rearing. *Developmental Psychobiology 18(2),* 115-123.

MacKinnon, JR. & MacKinnon, KS. (1980). Niche differentiation in a primate community. In *Malaysian forest primates : ten years' study in tropical rain forest.* (ed. DJ Chivers), Plenum Press, New York.

Mahon, TE., Kaiser, GW. & Burger, AE. (1992). The role of marbled marrelets in mixed-species feeding flocks in British Colombia. *Wilson Bull. 104(4),* 738-743.

Mallinson, JJ. (1975). Breeding marmosets in captivity. In *Breeding Endangered Species in Captivity,* (ed. RD. Martin), pp 203-212. Academic Press, London.

Mallinson, JJ. (1982). Cage furnishings and environments for primates : with special reference to marmosets and anthropoid apes. *Nat. Fed. Zoological Gardens of G.B and Ireland, pull-out suppl. 12* , Spring 1982.

Marler, P. (1978). A comparison of vocalizations of red-tailed monkeys & blue monkeys, *Cercopithecus ascanius* and *C. mitis,* in Uganda. *Z. Tierpsychol. 33,* 223-247.

Martin, P. & Bateson, P. (1986). *Measuring Behaviour.* Cambridge University Press, Cambridge.

Martins, E. Schneider, H. Leao, VF. (1987). Synopy and troops association between *Callithrix* and *Saguinus* from Rondonia, Brazil. *Int. J. Primatol. 8(5),* 527 (Abstract).

Masataka, N. (1981a). A field study of the social behavior of Goeldi's monkeys (*Callimico goeldii*) in North Bolivia. I. Group composition, breeding cycle, and infant development. *Kyoto Univ. Overseas Res. Rep. New World Monkeys (1981),* 23-32.

Masataka, N. (1981b). A field study of the social behavior of Goeldi's monkeys(*Callimico goeldii*) in North Bolivia. II. Grouping pattern and intragroup relationships. *Kyoto Univ. Overseas Res. Rep. New World Monkeys (1981),* 33-41.

Masataka, N. (1993). Effects of experience with live insects on the development of fear of snakes in squirrel monkeys, *Saimiri sciureus. Anim. Behav. 46,* 741-746.

McGraw, S. (1994). Census, habitat preference, and polyspecific association of six monkeys in the Lomako forest, Zaire. *Am. J. Primatol. 34,* 295-307.

McGrew, WC. (1986). Kinship terms and callitrichid mating patterns: a discussion note. *Primate Eye 30,* 25-26.

McGrew, WC. (1987). Helpers at the nest-box, or, are cotton-top tamarins really Florida scrub jays ? *Prim. Rep. 18,* 21-26.

McGrew, WC. (1988). Parental division of infant caretaking varies with family composition in cotton-top tamarins. *Anim. Behav. 36,* 285-286.

McGrew, WC. & McLuckie, EC. (1986). Philopatry and dispersion in the cotton-top tamarin, *Saguinus (o.) oedipus*: an attempted laboratory simulation. *Int. J. Primatol. 7,* 399-420.

McKenzie, SM. Chamove, AS. & Feistner, ATC. (1986). Floor-coverings and hanging screens alter arboreal monkey behavior. *Zoo Biol. 5,* 339-348.

Menzel, EW. (1962). Individual differences in the responsiveness of young chimpanzees to stimulus size and novelty. *Percept. Mot. Skills 15,* 127-134.

Menzel, EW. (1969). Naturalistic and experimental approaches to primate behaviour. In *Naturalistic viewpoints in psychological research,* (ed. EP Willems & HL Raush), Holt, Rinehart & Winston, New York.

Menzel, CW. (1980). Head-cocking and visual perception in primates, *Anim, Behav. 28,* 151-159.

Menzel, EW. & Menzel, CR. (1979). Cognitive, developmental and social aspects of responsiveness to novel objects in a family group of marmosets (*Saguinus fuscicollis*). *Behaviour 70,* 251-279.

Menzel, CR. & Menzel, EW. (1980). Head-cocking and visual exploration in marmosets (*Saguinus fuscicollis*). *Behavior 75,* 219-234.

Menzel, EW. & Juno, C. (1982). Marmosets (*Saguinus fuscicollis*) : are learning sets learned ?. *Science 217*, 750-752.

Menzel, EW. & Juno, C. (1984). Social foraging in marmoset monkeys and the question of intelligence. In : *Animal intelligence : Proceedings of a Roy. Soc. Discussion Meeting, 6/7 June 1984.*, *Vol 7,* (ed L. Weiskrantz), pp 145-158., Oxford.

Menzel, EW. & Juno, C. (1985).Social foraging in marmoset monkeys and the question of intelligence. *Phil. Trans. Roy. Soc. Lond. B 308,* 145-158.

Metcalfe, NB. (1984). The effects of mixed-species flocking on the vigilance of shorebirds : who do they trust ?. *Anim. Behav. 32,* 986-993.

Milinski, M. (1977). Experiments on the selection by predators against spatial oddity of their prey. *Z. Tierpsychol. 43,* 311-325.

Milinski, M. (1979). An evolutionary stable feeding strategy in sticklebacks. *Z. Tierpsychol. 51,* 36-40.

Milinski, M. (1984). A predator's costs of overcoming the confusion-effect of swarming prey. *Anim. Behav. 32,* 233-242.

Millar, SK., Evans, S. & Chamove, AS. (1988). Older offspring contact novel objects soonest in callitrichid families. *Biology of Behav. 13(2),* 82-96.

Mitani, M. (1991). Niche overlap and polyspecific associations among sympatric *Cercopithecids* in the Campo animal reserve, southwestern Cameroon. *Primates 32(2),* 137-151.

Mittermeier, RA. (1973). Group activity and population dynamics of howler monkeys on Barro Colorado Island. *Primates 14,* 1-19.

Mittermeier, RA, Rylands, AB & Coimbra-Filho AF (1988). Systematics: species and subspecies - an update. In :*Ecology and Behavior of Neotropical Primates, Vol. 2,* (ed. RA. Mittermeier, AB Rylands, AF Coimbra-Filho & GAB Fonseca), pp 13-75. World Wildlife Fund, Washington DC.

Mittermeier, RA. Kinzey, WG. Mast, RB. (1989). Neotropical primate conservation. *J. Human Evol. 18,* 597-610.

Montes de Oca, I. (1989). *Geografiya y recursos naturales de Bolivia, 2nd Ed.*, Ministeiro de Education y Cultura, La Paz, Bolivia.

Morse, DH. (1970). Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monographs 40,* 119-168.

Morse, DH. (1977). Feeding behaviour and predator avoidance in heterospecific groups. Bioscience 27, 332-339.

Morse, DH. (1978). Structure and foraging patterns of flocks of tits and associated species in an English woodland during winter.*Ibis 120,* 298-311.

Morse, DH. (1980). *Behavioural mechanisms in ecology.* Harvard University Press, Cambridge M.A.

Moodie, E. & Chamove, AS. (1990). Brief threatening events beneficial for captive tamarins ? *Zoo Biol. 9,* 275-286.

Moody, MI. & Menzel, EW. (1976). Vocalizations and their behvioural contexts in the tamarin, *Saguinus fuscicollis. Folia primatologica 25,* 73-94.

Moore, K., Cleland J. & McGrew WC. (1991). Visual encounters between families of cotton-top tamarins, *Saguinus (o.) oedipus. Primates 32(1),* 23-33.

Morrison, T,. Brown, A. & Rose, A. (1985). *Lizzie : a Victorian lady's Amazon adventure.* British Broadcasting Corporation, London.

Moynihan, M. (1962). The organization and probable evolution of some mixed species flocks of Neotropical birds. *Smith. Miscell. Collect. 143,* 1-140.

Moynihan, M. (1970). Some behavior patterns of platyrrhine monkeys. II. *Saguinus geoffroyi* and some other tamarins. *Smith. Contrib. Zool. 28,* 1-77.

Moynihan, M. (1976). *The New World Primates.* Princeton University Press, Princeton, New Jersey.

Neil, SR. & Cullen, JM. (1974). Experiments on whether schooling by their prey affects the hunting behaviour of cephalapods and fish predators. *J. Zool. Lond. 172,* 549-569.

Neville, MK., Castro, N., Marmol, A. & Revilla, J. (1976). Censusing primate populations in the reserved area of the Pacaya and Samiria rivers, Department Loreto, Peru. *Primates 17,* 151-181.

Neville, MK., Glander, KE., Braza, F. & Rylands, AB. (1988). The howling monkeys, genus *Alouatta.* In *Ecology and Behavior of Neotropical Primates, Vol. 2,* (eds. RA. Mittermeier, AB Rylands, AF Coimbra-Filho & GAB Fonseca), pp 349-454. World Wildlife Fund, Washington DC.

Neyman, PF. (1978). Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In : *Biology and Conservation of the Callitrichidae,* (ed. DG Kleiman), pp 39-71. Smithsonian Institution Press, Washington D.C.

Neyman, PF. (1980). *Ecology and Social Organization of the Cotton-top Tamarin* (Saguinus oedipus). PhD thesis, University of California, Berkeley. University Microfilms International, Ann Arbor, Michigan.

Nichol, J. (1985). *The mighty rainforest*. David & Charles, London.

Nishimura, A., da Fonseca, GAB., Mittermeier, RA., Young, Al,. Strier, KB. & Valle, CMC. (1988). The muriqui, genus *Brachyteles.* In *Ecology and Behavior of Neotropical Primates, Vol. 2,* (ed. RA. Mittermeier, AB Rylands, AF Coimbra-Filho & GAB Fonseca), pp 577-610. World Wildlife Fund, Washington DC.

Norconk, MA. (1986). *Interactions between primate species in a neotropical forest : mixed species troops of Saguinus mystax and S.fuscicollis (Callitrichidae).* Unpublished PhD. thesis, University of California, Los Angeles, (Abstract).

Norconk, MA. (1990a). Introductory remarks : ecological and behavioural correlates of polyspecific primate troops. *Am. J. Primatol. 21,* 81-85.

Norconk, MA. (1990b). Mechanisms promoting stability in mixed *Saguinus mystax* and *Saguinus fuscicollis* troops. *Am. J. Primatol.,* 21:159-170

Oates, JF. & Whitesides, GH. (1990). Association between olive colobus (*Procolobus verus*), Diana guenons (*Cercopithecus diana*), and other forest monkeys in Sierra Leone. *Am. J. Primatol. 21,* 129-146.

Ogden, JD. & Wolfe, LG. (1979). Reproduction of wild caught marmosets (*Saguinus labiatus labiatus*) under laboratory conditions. *Lab. Anim. Sci. 29,* 545-546.

O'Neill, PL. Novak, MA, Suomi, SJ. (1991). Normalizing laboratory-reared rhesus macaque (*Macaca mulatta*) behavior with exposure to complex outdoor enclosures. *Zoo Biology 10,* 237-245.

Paquette, D. & Prescott, J. (1988). Use of novel objects to enhance environments of captive chimpanzees. *Zoo Biol. 7(1),* 15-23.

Park, T. (1954). Experimental studies of interspecific competition in two species of *Tribolium. Physiol. Zool. 27,* 177-238.

Passingham, RE. (1975). The brain and intelligence. *Brain, Behav. & Evol 11(1),* 1-15.

Pennington R. *et al.,* (1988). *Oxford University Expedition '88, to Bolivia.* Unpublished Report to Centro de Desarollo Forestal (CDF), La Paz, Bolivia.

Peres, C. (1989). Exudate-eating by wild golden lion tamarins, *Leontopithecus rosalia. Biotropica 21,* 287-288.

Peres, C. (1991). *Ecology of mixed-species groups of tamarins in Amazonian terra firme forests.* Unpublished PhD. Thesis, University of Cambridge.

Peres, C. (1992a). Prey-capture benefits in a mixed species group of Amazonian tamarins, *Saguinus fuscicollis & S. mystax. Behav. Ecol. Sociobiol. 31,* 339-347.

Peres, C. (1992b). Consequences of joint-territoriality in a mixed-species group of tamarin monkeys. *Behaviour 123 (3-4),* 220-246.

Peres, C. (1993a). Diet and feeding ecology of saddle-back (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins in an Amazonian terra firme forest. *J. Zool. Lond. 230,* 567-592.

Peres, C. (1993b). Structure and spatial organization of an Amazonian terra firme forest primate community. *J. Trop. Ecol. 9(3),* 259-276.

Peres, C. (1993c). Notes on the ecology of buffy saki monkeys (*Pithecia albicans,* Gray 1860) : a canopy seed predator. *Am. J. Primatol. 31,* 129-140.

Peres, C. (1993d). Anti-predator benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica 61*, 61-76.

Peres, C. (1993e). Notes on the primates of the Jurua river, western Brazilian Amazonia. *Folia Primatologica 61*, 97-103.

Peres, C. (1994). Primate responses to phenological changes in Amazonian terra firme forest. *Biotropica 26(1)*, 98-112.

Peters, G. & Nogge, G. (1986). Occasional field observations of interspecific social grooming in African Cercopithecidae (Mammalia : Primates). Z. *Sangetierk 51*, 60-62 (Abstract).

Pilleri, G. & Knuckley, J. (1969). Behavior patterns of some Delphinidae observed in the western Mediterranean. Z. *Tierpsychol. 26*, 48-72.

Pires, JM. & Prance, GT. (1985). The vegetation types of the Brazilian Amazon. In *Key environments : Amazonia.* (ed. GT Prance & TE Lovejoy). Pergamon Press, Oxford.

Pitcher, TJ. (1986). The functions of shoaling behaviour. In *The behaviour of teleost fishes.* (ed. TJ Pitcher), pp 294-337, Croom Helm, London.

Podolsky, RD (1990). Effects of mixed-species association on resource use by *Saimiri sciureus and Cebus apella. Am. J. Primatol. 21*, 147-158.

Pook, AG. & Pook, G. (1981). A field study of the socio-ecology of the Goeldi's monkey (*Callimico goeldii*) in northern Bolivia. *Folia primatologica 35*, 288-312.

Pook, AG. & Pook, G. (1982). Polyspecific association between *Saguinus fuscicollis, Saguinus labiatus, Callimico goeldii*, and other primates in north-western Bolivia. *Folia primatologica 38*, 196-216.

Poole, TB. (1990). Environmental enrichment for marmosets. *Anim. Technology 42(2)*, 81-86.

Poole, TB. (1991a).Criteria for the provision of captive environments. In *Primate responses to environmental change* , (ed. HO Box), pp 357-374, Chapman & Hall, London.

Poole, TB. (1991b). The behavioural needs of captive primates : can they be identified ? In *Primatology Today,* (ed. Akiyoshi, Ehara *et al.*), pp 659-662, Elsiver Scientific.

Powell, GVN. (1974). Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*). in relation to predation and foraging. *Anim. Behav. 22*, 501-505.

Powell, GVN. (1989). On the possible contribution of mixed species flocks to species richness in Neotropical avifaunas. *Behav. Ecol. Sociobiol. 24*, 387-393.

Price, EC. (1990a). *Reproductive strategies of cotton-top tamarins.* Unpublished PhD Thesis, University of Stirling.

Price, EC. (1990b). Parturition and perinatal behaviour in captive cotton-top tamarins (*Saguinus oedipus*). *Primates 31(4)*, 523-535.

Price, EC. (1991). Stability of wild callitrichid groups. *Folia primatologica 57(2),* 111-114.

Price, EC. (1992). The costs of infant carrying in captive cotton-top tamarins. *Am. J. Primatol. 26,* 23-33.

Price, EC. & McGrew, WC. (1990). Cotton-top tamarins (*Saguinus (o.) oedipus*) in a semi-naturalistic captive colony. *Am. J. Primatol. 20,* 1-12.

Price, EC., Feistner, ATC., Carroll, JB. & Young, JA. (1989). Establishment of a free-ranging group of cotton-top tamarins, *Saguinus oedipus*, at the Jersey Wildlife Pres. Trust. *Dodo, J. Jersey Wildl. Pres. Trust, 26,* 60-69.

Price, EC., McGivern, AM. & Ashmore, L. (1991). Vigilance in a group of free-ranging cotton-top tamarins (*Saguinus oedipus*). *Dodo, J. Jersey Wildl. Pres. Trust, 27,* 41-49.

Price, EC. & Evans. S. (1991). Terminology in the study of callitrichid reproductive strategies. *Anim. Behav. 42(6),* 1025-1027.

Pruetz, JD. & Garber, PA. (1991). Patterns of resource utilization, home range overlap, and intergroup encounters in moustached tamarin monkeys. *Am. J. Phys. Anthro. suppl 12,* 146 (Abstract).

Pryce, CR. (1988). Individual and group effects on early caregiver-infant relationships in red-bellied tamarin monkeys. *Anim. Behav. 36,* 1455-1464.

Pulliam, HR. (1973). On the advantages of flocking. *J. Theor. Biol. 38,* 419-422.

Pulliam, HR. & Caraco, TC. (1984). Living in groups : is there an optimal group size ?. In *Behavioural ecology : an evolutionary approach,* 2nd ed. (ed. JR Krebs & NB Davies). pp 122-147. Blackwell, London.

Pulliam, HR. & Millikan,GC. (1982). Social organization in the non-reproductive season. *Avian Biol. 6,* 123-147 (Abstract).

Quenette, PY. (1990). Functions of vigilance in mammals ; a review. *Acta Oecol. 11,* 801-818.

Quenette, PY. & Desportes, JP. (1992). Temporal and sequential structure of vigilance behavior of wild boars (*Sus scrofa*). *J. Mammology 73(3),* 535-540.

Ramirez, M (1984). Population recovery in the moustached tamarin (*Saguinus mystax*): management strategies and mechanisms of recovery. *Am. J. Primatol. 7,* 245-259.

Ramirez, M (1989). *Feeding ecology and demography of the moustached tamarin, Saguinu mystax, in northeastern Peru.* Unpublished PhD Thesis, City University of New York, New York, (Abstract).

Rasa, OAE. (1983). Dwarf mongoose and hornbill mutualism in the Taru desert, Kenya. *Behav. Ecol. Sociobiol. 12,* 181-190.

Redshaw, ME. & Mallinson, JJC. (1991). Stimulation of natural patterns of behaviour : studies with golden lion tamarins and gorillas. In *Primate responses to environmental change* , (ed. HO Box), pp 217-238, Chapman & Hall, London.

Renner, MJ., Bennet, AJ., Ford, ML. & Pierre, PJ. (1992). Investigation of inanimate objects by the greater bushbaby (*Otolemur garnetti*). *Primates 33(3),* 315-327.

Richard, A. (1970). A comparative study of the activity patterns and behavior of *Alouatta villosa* and *Ateles geoffroyi. Folia primatologica 12,* 241-263.

Rodman, PS. (1973). Synecology of Bornean primates I. A test for interspecific interactions in spatial distribution of five species. *Am. J. Phys. Anthro. 38,* 655-660.

Roeder, EI., Timmermans, PJA. & Vossen JMH. (1989). Effects of rearing and exposure condition upon the acquisition of phobic behaviour in cynomolgus monkeys. *Behav. Res. Theory 27(3),* 221-231.

Roosmalen, MGM van (1985). *Fruits of the Guianan flora.* Institute of Systematic Botany, Utrecht.

Roosmalen, MGM van, & Klein, LL. (1988). The spider monkeys, genus *Ateles.* In *Ecology and Behavior of Neotropical Primates, Vol. 2,* (eds. RA. Mittermeier, AB Rylands, AF Coimbra-Filho & GAB Fonseca), pp 455-537. World Wildlife Fund, Washington DC.

Rothe, H. & Darms, K. (1993). the social organization of marmosets ; a critical evaluation of recent concepts. In : *Marmosets and tamarins. systematics, behaviour and ecology.,* (ed. AB Rylands), pp 176-199, Oxford University Press, Oxford.

Rowell, T. (1979). How would we know if social organization were not adaptive ?. In *Primate ecology and human origins : ecological influences on social organization.* (ed. IS Bernstein & EO Smith), pp 1-22, Garland, New York.

Roy, MA., Hennig, CW., Hill, EN. & Walker, ML. (1981). Subspecies differences in curiosity and general activity for developing squirrel monkeys. *Developmental Psychobiol. 14(1),* 55-58.

de Ruiter, JR. (1986). The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (*Cebus olivaceus*). *Behaviour 98,* 240-258.

Ruth B. (1991). Social behavior of free-living tamarin monkeys (*Saguinus mystax*) on Padre Isla, Peru. *Am. J. Phys. Anthro. Suppl 12 ,* 156 (Abstract).

Rylands, AB. (1981). Preliminary field observations on the marmoset, *Callithrix humeralifer intermedius* (Hershkovitz, 1977) at Dardanelos, Rio Arapuana, Mato Grosso. *Primates 22,* 46-59.

Rylands, AB. (1984). Exudate eating and tree-gauging by marmosets (Callitrichidae , Primates). In *Tropical rain forest : The Leeds Symposium.* (ed AC Chadwick & SL Sutton).pp 155-168, Leeds Philosophical and Literary Society, Leeds.

Rylands, AB. (1987). Primate communities in Amazonian forests: their habitats and food resources. *Experientia 43,* Birkhauser Verlag, Basel, Switzerland.

Rylands, AB. (1989). Sympatric Brazilian callitrichids : the black tufted-ear marmoset, *Callithrix kuhli,* and the golden-headed lion tamarin, *Leontopithecus chrysomelas. J. Human Evol. 18,* 679-695.

Rylands, AB. (in press). Habitat and the evolution of social and reproductive behaviour in Callitrichidae. *Am. J. Primatol.*

Rylands, AB. & Keuroghlian, A. (1988). Primate populations in continuous forest and forest fragments in central Amazonia. *Acta Amazonica 18(3-4),* 291-307.

Rylands, AB. & de Faria, DS. (1993). Habitats, feeding ecology and home range size in the genus *Callithrix.* In : *Marmosets and tamarins. systematics, behaviour and ecology.,* (ed. AB Rylands), pp 262-272, Oxford University Press, Oxford.

Rylands AB., Coimbra-Filho AF. & Mittermeier RA (1993). Systematics, geographic distribution, and some notes on the conservation status of the Callitrichidae. In : *Marmosets and Tamarins. Systematics, Behaviour and Ecology.,* (ed. AB. Rylands), pp 11-77, Oxford University Press, Oxford.

Rylands, AB., da Cruz MAOM. & Ferrari, SF (1989). An association between marmosets and army ants in Brazil. *J. Trop. Ecol. 5,* 113-116.

Sasvari, L. (1992). Great tits benefit from feeding in mixed-species flocks : a field experiment. *Anim. Behav. 43,* 289-296.

Savage, A., Dronzek, LA.& Snowdon, CT. (1987). Color discrimination by the cotton-top tamarin (*Saguinus oedipus oedipus*) and its relation to fruit coloration. *Folia primatologica 49,* 57-69.

Savage, A., Snowdon, CT., Giraldo H. & Rodriguez,JV. (1989). The ecology of the cotton-top tamarin (*Saguinus o. oedipus*) in Colombia - Progress Report, October 1989. In, *British Is. & Ireland: Regional Studbook Cotton-topped Tamarin* (Saguinus o. oedipus*), No. 4 (1989)*, (ed. R Colley).

van Schaik, CP. (1983). Why are diurnal primates living in groups ?. *Behaviour 87,* 120-143.

van Schaik, CP. & van Hooff, J. (1983). On the ultimate causes of primate social systems. *Behaviour 85,* 91-117.

van Schaik, CP. & Horstermann, M. (1994). Predation risk and the number of adult males in a primate group : a comparative test. *Behav. Ecol. Sociobiol. 35,* 261-272.

van Schaik, CP. & Mitrasetta, T. (1992). Changes in the behaviour of wild long-tailed macaques (*Macaca fascicularis*) after encounters with a model python. *Folia primatologica 55,* 104-108.

van Schaik, CP. & van Noordwijk, MA. (1985). Evolutionary effect of the absence of felids on the social organisation of the macaques on the island of Simeule (*Macaca fascicularis fusca,* Miller 1903). *Folia primatologica 44,* 138-147.

van Schaik, CP., van Noordwijk, MA., Warsono, B. & Sutriono, E. (1983). Party size and early detection of predators in Sumatran forest primates. *Primates 24,* 211-221.

Schwartz, GG. & Rosenblum, LA. (1980). Novelty, arousal and nasal marking in the squirrel monkey. *Behavioral & Neural Biol. 28(1),* 116-122.

Seyfarth, R. & Cheney, D. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behav. 40,* 754-764.

Sherman, PW (1981). Kinship, demography and Belding's ground squirrel nepotism. *Behav. Ecol. Sociobiol. 8*, 251-259.

Sinclair, ARE. (1985). Does interspecific competition or predation shape the African ungulate community ?. *J. Anim. Ecol. 54*, 899-918.

Siegel, S. & Castellan, NJ. (1988). *Nonparametric Statistics for the Behavioral Sciences. 2nd edition.* McGraw-Hill, London.

Silva-Lopez,G. Jimenez-Huerta, J. & Benitez-Rodriguez, J. (1993). Availability of Resources to Primates and Humans in a Forest Fragment of Sierra de Santa Martha, Mexico. *Neotropical Primates, 1(4)*, 3-5.

Snowdon, CT. Savage, A. & McConnel, PB (1985). A breeding colony of cotton-top tamarins (*Saguinus oedipus*). *Lab. Anim. Sci. 35*, 477-480.

Snowdon, CT. & Soini, P. (1988). The tamarins, genus *Saguinus.* In *Ecology and Behavior of Neotropical Primates, Vol. 2*, (ed. RA Mittermeier, AB Rylands, AF Coimbra-Filho & GAB Fonseca), pp 223-298, World Wildlife Fund, Washington DC.

Snowdon, CT. & Suomi, SJ.(1982). Paternal behaviour in primates. In *Child Nurturance, Vol 3*, (ed. HE Fitzgerald, JA Mullins, P Gage), pp 63-108, Plenum, New York.

Soini, P. (1993). The ecology of the pygmy marmoset, *Cebuella pygmaea* : some comparisons with two sympatric tamarins. In : *Marmosets and Tamarins. Systematics, Behaviour and Ecology.* (ed. AB. Rylands), pp 257-261, Oxford University Press, Oxford.

Soini, P. (1987). Ecology of the saddle-back tamarin *Saguinus fuscicollis illigeri* on the Río Pacaya, northeastern Peru. *Folia primatologica 49*, 11-32.

Southwick, CH. & Southwick, KL. (1983). Polyspecific groups of macaques on the Kawloon Peninsula, New Territories, Hong Kong. *Am. J. Primatol. 5*, 17-24.

Stacey, PB.(1986). Group size and foraging efficiency in yellow baboons. *Behav. Ecol. Sociobiol. 18*, 175-187.

Stanford, CB. (1989). Predation on capped langurs (*Presbytes pileata*), by cooperatively hunting jackals (*Canis aureus*). *Am. J. Primatol. 19*, 53-56.

Stevenson, MF. & Rylands, AB. (1988). The marmosets, genus *Callithrix.* In *Ecology and Behavior of Neotropical Primates, Vol. 2*, (ed. RA Mittermeier, AB Rylands, AF Coimbra-Filho & GAB Fonseca), pp 131-222 , World Wildlife Fund, Washington DC.

Struhsaker, TT. (1981). Polyspecific association among tropical rainforest primates. *Z. Tierpsychol. 57*, 268-304.

Struhsaker, TT. & Leakey, M. (1990). Prey selectivity by crowned hawk-eagles on monkeys in the Kibale forest, Uganda. *Behav. Ecol. Sociobiol. 26*, 435-443.

Sullivan, KA. (1984). Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour 91(4)*, 294-311.

Sullivan, KA. (1985). The advantages of social foraging in downy woodpeckers. *Anim. Behav. 32,* 16-22.

Sussman, RW. & Garber, PA. (1987). A new interpretation of the social organization and mating system of the Callitrichidae. *Int. J. Primatol. 8,* 73-92.

Sussman, RW. & Kinzey, WG. (1984). The ecological role of the Callitrichidae: a review. *Am. J. Phys. Anth. 64,* 419-449.

Tardif SD.(1984). Social influences on sexual maturation of female *Saguinus oedipus. Am. J. Primatol. 6,* 199-209.

Tardif SD., Richter, CB. & Carson, RL. (1984). Effects of sibling-rearing experience on future reproductive success in two species of Callitrichidae. *Am. J. Primatol. 6,* 377-380.

Tardif SD, Harrison, ML. & Simek, MA. (1993). Communal infant care in marmosets and tamarins : relation to energetics, ecology and social oranization. In : *Marmosets and Tamarins. Systematics, Behaviour and Ecology.*, (ed. AB. Rylands), pp 220-234, Oxford University Press, Oxford.

Terborgh, J. (1983). *Five New World Primates.* Princeton University Press, Princeton, New Jersey.

Terborgh, J. (1986). The social systems of New World primates: an adaptionist view. In *Primate Ecology and Conservation,* (ed. JG Else & PC Lee), pp 199-211. Cambridge University Press, New York.

Terborgh, J. (1990). Mixed flocks and polyspecific associations : costs and benefits of mixed groups to birds and monkeys. *Am. J. Primatol. 21,* 87-100.

Terborgh, J. & Goldizen, AW. (1985). On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). *Behav. Ecol. Sociobiol. 16,* 293-299.

Terborgh, J. & Janson, CH. (1986). The socioecology of primate groups. *Ann. Rev. of Ecol. and Sytstem. 17,* 111-135.

Terborgh, J. & Stern, M. (1987). The surreptitious life of the saddle-backed tamarin. *Am. Sci. 75,* 260-269.

Thompson, DBA. & Barnard, CJ. (1983). Anti-predator responses in mixed species associations of lapwings, golden plovers and black headed gulls. *Anim. Behav. 31,* 585-593.

Thorington, RW. Jr (1988). Taxonomic status of *Saguinus tripartitus* (Milne-Edwards, 1878). *Am. J. Primatol. 15,* 367-371.

Underwood, R. (1982). Vigilance behaviour in grazing African antelopes. *Behaviour 79,* 81-107.

Vine, I. (1973). Detection of prey flocks by predators. *J. Theor. Biol. 40,* 207-210.

Visalberghi, E. (1988). Responsiveness to objects in 2 social groups of tufted capuchin monkeys (*Cebus apella*). *Am. J. Primatol. 15,* 349-360.

de Vivo, M (1985). On some monkeys from Rondônia, Brasil (Primates: Callitrichidae, Cebidae). *Papéis Avulsos de Zoologia 36,* 103-110.

Vochteloo, JD., Timmermans, PJ., Duijghuisen, JA. & Vossen, JM.(1991). Responses to novelty in phobic and non-phobic cynomolgus monkeys : The role of subject characteristics and object features. *Behav. Res. & Therapy 29(6),* 531-538.

Vogt, JL. (1978). The social behavior of a marmoset (*Saguinus fuscicollis*) group. II. Behavior patterns and social interaction. *Primates 19,* 287-300.

Vogt, JL., Carlson, H. & Menzel E. (1978). Social behavior of a marmoset (*Saguinus fuscicollis*) group. I. Parental care and infant development. *Primates 19,* 715-726.

Ward, P. & Zahavi, A. (1973). The importance of certain assemblages of birds as "information centres" for food finding. *Ibis 115,* 517-534.

Waser PM. (1977). Feeding, ranging, and group size in the mangabey *Cercocebus albigena.* In *Primate ecology.* (ed TH Clutton-Brock), Academic Press, London.

Waser PM. (1980). Polyspecific associations of *Cercocebus albigena* : Geographic variation and ecological correlates. *Folia primatologica 33,* 57-76.

Waser PM. (1982). Primate polyspecific associations. Do they occur by chance ?. *Anim. Behav. 30,* 1-8.

Waser PM. (1984). "Chance" and mixed-species associations. *Behav. Ecol. Sociobiol. 15,* 197-202.

Waser PM. (1987). Interactions among primate species. In : *Primate Societies* (Eds. BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham & TT Struhsaker). University of Chicago Press, London.

Welker, C. & Schafer-Witt, C. (1989). On the carrying behaviour of basic South American primates. *Human Evol. 2(5),* 459-473.

Whitesides, GH. (1989). Interspecific associations of Diana monkeys, *Cercopithecus diana* in Sierra Leone, west Africa ; Biological significance or chance ?. *Anim. Behav. 37,* 760-776.

Wolf, NG. (1985). Odd fish abandon mixed-species groups when threatened. *Behav. Ecol. Sociobiol. 17,* 47-52.

Wolfe LG., Deinhardt, F., Ogden, JD., Adams, MR. & Fisher, LE. (1975). Reproduction of wild-caught and laboratory-born marmoset species used in biomedical research (*Saguinus* sp., *Callithrix jacchus*). *Lab. Anim. Sci. 25,* 802-813.

Wrangham, RW. (1983). Social relationships in comparative perspective. In *Primate social relationships : An integrated approach.* (ed. RA Hinde), Blackwell, Oxford.

Wrangham, RW. (1987).Evolution of social structure. In *Primate societies* , (Ed BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham & TT Struhsaker), University of Chicago Press, Chicago.

Wrangham, RW. (1980). An ecological model of female-bonded primate groups. *Behaviour 75,* 262-300.

Wrangham, RW., Gittleman, JL. & Chapman, CA. (1993). Constraints on group size in primates and carnivores : population density and day range as assays of exploitation competition. *Behav. Ecol. Sociobiol. 32,* 199-209.

Xanten WA. (1990).Marmoset behaviour in mixed-species exhibits at the National Zoological Park, Washington.*Int. Zoo Yb. 29,* 143-148.

Xanten WA. (1992).Mixed-species exhibits - are they worth it ?.*AAZPA 1992 Regional Proceedings* 59-61.

Yamamoto, ME. (1993). From dependence to sexual maturity : the behavioural ontogeny of Callitrichidae. In : *Marmosets and Tamarins. Systematics, Behaviour and Ecology.* (ed. A.B. Rylands), pp 235-256, Oxford University Press, Oxford.

Yoneda, M. (1981). Ecological studies of *Saguinus fuscicollis* and *Saguinus labiatus* with reference to habitat segregation and height preference. *Kyoto Univ. Overseas Res. Rep. New World Monkeys 1981,* 43-50.

Yoneda, M. (1984a). Ecological study of the saddle backed tamarin (*Saguinus fuscicollis*) in northern Bolivia. *Primates 25,* 1-12.

Yoneda, M. (1984b). Comparative studies on vertical separation, foraging behavior and traveling mode of saddle-backed tamarins (*Saguinus fuscicollis*) and red-chested moustached tamarins (*Saguinus labiatus*) in northern Bolivia. *Primates 25,* 414-422.

Ziegler, TE. Bridson, WE., Snowdon, CT. & Eman. S. (1987). Urinary gonadotropin and estrogen excretion during the postpartum estrus, conception, and pregnancy in the cotton-top tamarin (*Saguinus oedipus oedipus*). *Am. J. Primatol. 12,* 127-140.

Zullo, J. & Caine, NG. (1988). The use of sentinels in captive groups of red-bellied tamarins. *Am. J. Primatol. 14,* 455 (Abstract).

Appendix 1.

Sample copies of all checksheets used in experimental studies.

1) Experiment 4.A
2) Experiment 4.B
3) Experiment 5.1A/B
4) Experiment 5.1C
5) Experiment 5.2A
6) Experiment 5.2B
7) Experiment 6.1A
8) Experiment 6.1B
9) Experiment 6.2
10) Experiment 6.3

Checksheet 4.A

Mixed-Group Sl / Sf M / F Am/Pm Date

		O	W	N		O	T	H	E	R	0	0	50	1	1.5	2	2.5	3	3.5	4	4.5	Notes
	0	15	50	1M	1+	0	15	50	1M	1+	M	-50	-1M	-1.5	-2.0	-2.5	-3.0	-3.5	-4.0	-4.5	-5.0	
1 m																						
2 m																						
3 m																						
4 m																						
5 m																						
6 m																						
7 m																						

Checksheet 4.B

Mixed-Group Sl / Sf M / F

Am/Pm Date

	Behaviour	Position	Height	Orient.	Size	Same species	Other species	Dist from base	Quadrat	Notes
0										
1										
2										
3										
4										
5										
6										
7										
8										
9										
10 m										
11										
12										
13										
14										
15										
16										
17										
18										
19										
20 m										
21										
22										
23										
24										
25										
26										
27										
28										
29										
30 m										

Checksheet 5.1A/B

GROUP __________ START DATE__________

SPECIES_________ COMMENTS____________

OBJECT	EXIT	APPROACH	TOUCH	COMMENTS
TOP				
1				
2				
4				
5				
6				
MIDDLE				
1				
2				
3				
4				
5				
6				
FLOOR				
1				
2				
3				
4				
5				
6				

Checksheet 5.1C

MIXED GROUP __________ START DATE___________

COMMENTS_____________

OBJECT	EXIT	APPROACH	TOUCH	COMMENTS
TOP				
1 **SF**				
SL				
2 **SF**				
SL				
3 **SF**				
SL				
4 **SF**				
SL				
5 **SF**				
SL				
6 **SF**				
SL				
MIDDLE				
1 **SF**				
SL				
2 **SF**				
SL				
3 **SF**				
SL				
4 **SF**				
SL				
5 **SF**				
SL				
6 **SF**				
SL				
FLOOR				
1 **SF**				
SL				
2 **SF**				
SL				
3 **SF**				
SL				
4 **SF**				
SL				
5 **SF**				
SL				
6 **SF**				
SL				

Checksheet 5.2A

Species__________ Group__________ Time__________ Trial__________

Object__________ Food / NF Comments__________

	0	1	2	3	4	5		0	1	2	3	4	5
15							15						
30							30						
45							45						
1m							**6m**						
15							15						
30							30						
45							45						
2m							**7m**						
15							15						
30							30						
45							45						
3m							**8m**						
15							15						
30							30						
45							45						
4m							**9m**						
15							15						
30							30						
45							45						
5m							**10m**						

Checksheet 5.2B

Mixed group__________ Time__________ Trial__________

Object__________ Food / NF Comments__________

	Before	Appr.	Touch	Eat
S.fuscicollis				
S.labiatus				

	S. FUSC			S. LAB				S. FUSC			S. LAB		
	0	1	2	0	1	2		0	1	2	0	1	2
15							15						
30							30						
45							45						
1m							6m						
15							15						
30							30						
45							45						
2m							7m						
15							15						
30							30						
45							45						
3m							8m						
15							15						
30							30						
45							45						
4m							9m						
15							15						
30							30						
45							45						
5m							10m						

Checksheet 6.1A

Species ____________ **Subject** ____________ **Time** ________

Session ____________ **Weather** ____________

Look-up *Scanning* *Alarm Calling* *Comments*

0min ____

1m ____

2 ____

3 ____

4 ____

5min ____

6 ____

7 ____

8 ____

9 ____

10min ____

11 ____

12 ____

13 ____

14 ____

15min ____

16min ____

17 ____

18 ____

19 ____

20 ____

Checksheet 6.1B

Group ____________ **Subject** ____________ **Time** ________

Session ____________ **Weather** ____________

	Look-up		*Scanning*		*Alarms*	*Comments*
	S.fusc	*S.lab*	*S.fusc*	*S.lab*		
0min						
1m						
2						
3						
4						
5min						
6						
7						
8						
9						
10min						
11						
12						
13						
14						
15min						
16						
17						
18						
19						
20						

Checksheet 6.2

Species : ____________ **Object :** ______

Presentation : ________ **Time :** ____________

Comments : ____________

Alarm calls **0 <15 15-50 50-1M 1M+** **Approach** **Vigilance**

1min

2min

3min

4min

5min

6min

7min

8min

9min

10min

Checksheet 6. 3

Species _____ Group________

Stimuli______ Time_________

Time	Identity					Duration	Comments
	1	2	3	4	5		

Appendix 2.

Full list of objects that were selected to be used in experiment 5.1, novel object trials. Numbers are arbitrarily assigned to identify objects.

The 18 objects used for single species trials were;

Top area.

9. Grey PVC glove.
15. Hat shaped box.
24. Red socks.
17. Film box.
2. Stripy paper bag.
7. Green cardboard box.

Middle area.

3. Grey pen box.
23. Rubber key ring.
12. Blue stripy socks.
22. Squashed drinks can.
6. Small wicker basket.
18. Small toy dog.

Floor area.

9. Ointment box.
4. Pink candle.
20. Blue cardboard box.
11. Talcum powder tin.
10. Deodorant container.
21. Green beer bottle.

The 18 objects used for mixed-species trials were;

Top area.

28. Computer Disc.
29. Tooth Brush.
16. Blue comb.
30. Fruit Juice Carton.
31. Sea Shell.
32. Large Plastic Paperclip.

Middle area.

25. Stapler.
5. Triangular watch box.
8. Squashed toothpaste tube.
27. Sunglasses.
28. Plastic Disc.
33. Plastic Red Clown's Nose.

Floor area.

34. Small Alarm Clock.
37. Razor Stand.
35. Bottle Cork.
38. Soap Dish.
39. Rounded Tube Dispenser.
36. Hair Clasp.

Spare objects not used :

13. Swiss army knife.
40. Roll of Tape.
14. Round powder tin.
1. Blue card tube

Appendix 3

Full list of objects used during experiment 5.2.

Part 1 : Single Species Groups

“lose-shift” Objects

1. Squashed ice-cream tub.
2. Black paper bag.
3. Green plastic tube.

“Food” Objects

4. Squashed soup can.
5. Plant pot.
6. Iron “L-bend” pipe.

“Non-Food” Objects

7. Yoghurt Carton.
8. Small cardboard box.
9. Soap container.

“Food (Sl) / Non-Food (Sf)” Objects

10. White plastic tray.
11. Margarine tub.
12. Brown suede shoe.

“Non-Food(Sl) / Food(Sf)” Objects

13. Black aerosol lid.
14. Coloured cardboard box.
15. Piece of polystyrene.

Part 2 : Mixed Species Group

New “Non-Food” Objects

16. Wooden block.
17. Sealed plastic container.
18. Plastic hair comb.

New “Food” Objects

19. Ceramic cup.
20. Wooden box.
21. Black plastic tube.

Appendix 4

Full list of scores per trial during experiment 5.2A.

Group **SL1** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e
N					
1	9.5	9.5	12	10.5	0.8
2	15	13.5	10.5	13	1.3
3	12	13.5	8.5	11.3	1.5
Test	9	11	5.5	8.5	1.6
App					
1	4	35	43	27.3	11.9
2	3	18	36	19	9.5
3	4	9	3	5.3	1.9
Test	6	6	4	5.3	0.7
Tou					
1	4	71	48	41	19.6
2	4	21	37	20.7	9.5
3	4	10	4	6	2
Test	8	8	5	7	1

NF1	NF2	NF3	MEAN	St. e
3	6	5	4.7	0.9
5	1.5	9	5.2	2.2
3.5	1	2.5	2.3	0.7
1.5	0.5	0	0.7	0.4
71	7	18	32	19.8
21	15	2	12.7	5.6
3	-	105	54	51
21	-	-	27	-
72	8	19	32.7	19.9
26	-	3	14.5	11.5
4	-	312	173	169
22	-	-	22	-

	F/ NF1	F/ NF2	F/ NF3	MEAN	St. e
N					
1	10.5	10.5	16.5	12.5	2
2	14.5	13.5	11	13	1.1
3	13	10	12.5	11.8	0.9
Test	9	6.5	5.5	7	1
App					
1	6	3	27	12	7.6
2	8	4	18	10	4.2
3	6	5	6	5.7	0.3
Test	5	3	11	6.3	2.4
Tou					
1	7	5	28	13.3	7.4
2	8	6	21	11.7	4.7
3	7	6	7	6.7	0.3
Test	6	5	13	8	2.5

NF/ F1	NF/ F2	NF/ F3	MEAN	St. e
6	11.5	6	7.8	1.8
2.5	2	3.5	2.6	0.4
0.5	1.5	1.5	1.2	0.3
1	2.5	3	2.2	0.6
11	6	5	4	1.5
5	8	48	20.3	13.9
9	234	152	131.7	65.7
7	129	310	148.7	88
15	7	7	9.7	2.7
6	11	51	22.7	14.2
12	235	154	133.7	65.2
-	131	315	223	92

N = Mean number of visits per individual. **App** = duration to initial approach. **Tou** = Duration to initial touch. **St. e** = Standard error.

Group **SL2**　　Species *S. labiatus*　　Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	3	12.5	14	9.8	3.4
2	11.5	11	16	12.8	1.6
3	9	18	13.5	13.5	2.6
Test	7	9	9.5	8.5	0.8
App					
1	17	7	4	9.3	3.9
2	13	58	6	26.7	16.3
3	17	11	2	10	4.4
Test	27	11	15	17.7	4.8
Tou					
1	-	43	10	26.5	16.5
2	84	69	7	53.3	23.6
3	48	13	4	21.7	13.4
Test	68	14	17	33	17.5

NF1	NF2	NF3	MEAN	St. e
6.5	7	5.5	6.3	0.4
2.5	2.5	4	3	0.5
4.5	3.5	5	4.3	0.4
5	1	4.5	3.5	1.3
18	11	6	11.7	3.5
38	9	3	16.7	10.8
12	2	43	19	12.3
37	167	19	74.3	46.6
139	13	14	55.3	41.8
42	31	5	26	11
44	8	48	33.3	12.7
48	178	21	34.7	13.3

	F/ NF1	F/ NF2	F/ NF3	MEAN	St. e
N					
1	15.5	12	15.5	14.3	1.2
2	21.5	24.5	22.5	22.8	0.9
3	30	31.5	13.5	25	5.8
Test	14.5	10.5	13.5	12.8	1.2
App					
1	2	42	111	51.7	31.8
2	3	3	21	9	6
3	3	6	7	5.3	1.2
Test	1	3	4	2.7	0.9
Tou					
1	3	44	175	74	51.9
2	4	5	24	11	6.5
3	4	6	11	7	2.1
Test	2	5	6	4.3	2.1

NF/ F1	NF/ F2	NF/ F3	MEAN	St. e
10	8	14.5	10.8	1.9
7.5	6.5	4	6	1.0
5	3.5	4	4.2	0.4
1.5	6	5	4.2	1.4
4	3	5	4	0.6
4	16	7	9	3.6
3	158	11	57.3	50.4
-	31	166	98.5	67.5
6	4	6	5.3	0.7
11	33	9	17.7	7.7
4	161	13	59.3	50.9
-	-	168	168	-

Group **SL3** Species *S. labiatus* Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	16	12.5	13.5	14	1
2	13.5	10.5	13.5	12.5	1
3	15	9.5	16.5	13.7	2.1
Test	12	4.5	11.5	9.3	2.4
App					
1	13	63	3	26.3	18.6
2	2	17	3	7.3	4.8
3	2	4	2	2.7	1.3
Test	3	6	2	3.7	1.2
Tou					
1	14	64	7	28.3	17.9
2	4	25	6	11.7	6.7
3	5	5	3	4.3	0.7
Test	4	8	3	5	1.5

NF1	NF2	NF3	MEAN	St. e
3.5	8.5	4	5.3	1.6
1	2	1	1.3	0.3
3	3	2.5	2.8	0.2
0.5	3	3.5	2.3	0.9
11	1	1	7.7	3.3
4	1	65	23.3	20.9
9	2	330	113.7	108.2
4	5	-	4.5	0.5
13	4	4	7	3.5
6	3	-	4.5	1.5
-	3	-	3	
12	9	-	10.5	1.5

	F / NF1	F / NF2	F / NF3	MEAN	St. e
N					
1	16	5	10	10.3	3.2
2	25.5	23	18	18.8	2.2
3	20	24	8.5	17.5	4.6
Test	11.5	15.5	7	11.3	2.5
App					
1	2	216	108	108.7	61.8
2	3	4	7	4.7	1.2
3	3	6	3	4	1
Test	1	3	7	3.7	1.8
Tou					
1	2	217	110	109.7	62.1
2	5	9	9	7.7	1.3
3	4	9	4	5.7	1.7
Test	3	6	9	6	1.7

NF/ F1	NF/ F2	NF/ F3	MEAN	St. e
4	5.5	8.5	6	1.3
2	4.5	6.5	4.3	1.3
2.5	3	-	1.8	0.9
2.5	1.5	0	1.3	0.7
4	370	3	125.7	122.2
11	40	15	22	9.1
-	1	-	1	-
14	-	-	14	-
5	376	4	128.3	123.8
13	41	17	23.7	8.7
-	2	-	2	-
16	-	-	16	-

Group **SL4** Species *S. labiatus* Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	18	16	18	17.3	0.7
2	22	11	9.5	14.2	3.9
3	17	11.5	10.5	13	2
Test	11.5	7.5	7.5	8.8	1.3
App					
1	7	15	5	9	3.1
2	3	16	4	7.7	4.2
3	2	4	3	3	0.6
Test	4	5	5	4.7	0.3
Tou					
1	8	19	18	15	3.5
2	4	14	5	7.7	3.2
3	3	6	4	4.3	0.9
Test	6	8	8	7.3	0.7

NF1	NF2	NF3	MEAN	St. e
6.5	6.5	12	8.3	1.8
2.5	2.5	6.5	3.8	1.3
3.5	5.5	2	3.7	1
2	2	3.5	2.5	0.5
27	4	4	11.7	7.7
9	396	11	138.7	128.7
2	12	21	11.7	5.5
-	4	37	20.5	16.5
35	4	5	14.7	10.2
10	405	56	157	124.7
5	13	22	13.5	4.9
-	6	39	22.5	16.5

	F/ NF1	F/ NF2	F/ NF3	MEAN	St. e
N					
1	21	17.5	13	17.2	2.3
2	23	16	9	16	4
3	24.5	17.5	15.5	19.2	2.7
Test	21.5	13	14.5	16.3	2.6
App					
1	5	21	7	11	5
2	6	5	7	6	0.6
3	4	3	10	5.7	2.2
Test	3	4	5	4	0.6
Tou					
1	6	22	9	12.3	4.9
2	9	6	9	8	1
3	5	5	11	7	2
Test	3	8	7	6	1.5

NF/ F1	NF/ F2	NF/ F3	MEAN	St. e
6	10.5	5.5	7.3	1.6
3.5	5	4	4.2	0.4
3.5	9.5	1.5	4.8	2.4
2.5	3	0.5	2	0.8
22	6	7	11.7	5.2
4	18	103	41.7	30.9
9	8	-	8.5	0.5
5	12	416	144.3	135.9
48	8	8	21.3	13.3
8	20	109	45.7	31.9
16	9	-	12.5	3.5
8	15	419	147.3	135.9

Group **SL5** Species *S. labiatus* Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	14.2	12.4	14.4	13.7	0.6
2	16.8	14.2	10.2	13.7	1.9
3	20.4	17.4	20.4	19.4	1
Test	10.8	17.4	15.8	14.7	2
App					
1	31	4	2	12.3	9.4
2	2	1	1	1.3	0.3
3	2	2	1	1.7	0.3
Test	1	2	1	1.3	0.3
Tou					
1	55	6	7	22.7	16.2
2	4	3	2	3	0.6
3	4	3	2	3	0.6
Test	2	4	2	2.7	0.7

NF1	NF2	NF3	MEAN	St. e
12	12.2	13.4	12.5	0.4
9.2	6.8	4.6	6.9	1.3
4.2	4	8.4	5.5	1.4
6.8	1.8	5.2	4.6	1.5
3	7	1	3.7	1.8
2	3	1	2	0.6
1	2	2	1.7	0.3
1	5	8	4.7	2
4	14	3	7	3.5
4	7	3	4.7	1.2
8	5	3	5.3	1.5
3	7	11	7	2.3

	F / NF1	F / NF2	F / NF3	MEAN	St. e
N					
1	25	15.2	11.2	17.1	4.1
2	20.4	15.4	13.2	16.3	2.1
3	20.4	16.8	18.6	18.6	1
Test	9.4	16.2	11.8	12.5	2
App					
1	2	3	5	3.3	0.9
2	2	2	3	2.3	0.3
3	1	1	3	1.7	0.7
Test	4	1	2	2.3	0.9
Tou					
1	3	4	7	4.7	1.2
2	3	2	4	3	0.6
3	3	3	4	3.3	0.3
Test	5	3	3	3.7	0.7

NF/ F1	NF/ F2	NF/ F3	MEAN	St. e
6	12.2	12.8	10.3	2.2
5.4	10.2	8.2	7.9	1.4
6.8	5.4	7.8	6.7	0.7
3.6	5.6	2.4	3.9	0.9
1	3	3	2.3	0.7
2	4	3	3	0.6
9	5	3	5.7	1.8
4	1	3	2.7	0.9
3	4	4	3.7	0.3
3	5	4	4	0.6
10	7	4	7	1.7
5	2	4	3.7	0.9

Group **SL6** Species *S. labiatus* Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	15	17	16.5	16.2	0.2
2	16	20	16.5	17.5	1.3
3	18.5	15	15.5	16.3	1.1
Test	16	13.5	10	13.2	1.7
App					
1	3	5	8	5.3	1.5
2	6	3	3	4	1
3	5	6	6	5.7	0.3
Test	7	8	5	6.7	0.9
Tou					
1	5	6	11	7.3	1.9
2	8	4	5	5.7	1.2
3	6	7	9	7.3	0.9
Test	8	9	6	7.7	0.9

NF1	NF2	NF3	MEAN	St. e
11	16	7.5	11.5	2.5
6	4.5	9	6.5	1.3
6.5	3.5	4.5	4.8	0.9
7.5	3.5	4.5	5.2	1.2
6	8	3	5.7	1.5
9	101	8	39.3	30.8
138	41	21	66.7	36.1
48	5	-	26.5	21.5
7	9	4	6.7	1.5
10	102	9	40.3	30.8
140	106	22	89.3	35.1
49	5	-	27	22

	F/ NF1	F/ NF2	F/ NF3	MEAN	St. e
N					
1	13.5	17.5	18	16.3	1.4
2	19	29	19.5	22.5	3.3
3	22	17	18	19	1.5
Test	21	11	11	14.3	3.3
App					
1	3	5	13	7	3.1
2	9	11	7	9	1.2
3	9	7	4	6.7	1.5
Test	3	6	9	6	1.7
Tou					
1	3	8	16	9	3.8
2	11	12	8	10.3	1.2
3	11	8	6	8.3	15
Test	3	7	11	7	2.3

NF/ F1	NF/ F2	NF/ F3	MEAN	St. e
7.5	11	9	9.2	1
5.5	5	5.5	5.3	0.2
4	7	4	5	1
4	2	4	3.3	0.7
7	36	31	24.7	9
4	278	153	145	79.2
15	6	218	76.3	65.9
60	11	-	35.5	24.5
8	38	33	26.3	9.3
5	281	156	147.3	79.8
17	7	210	78	66
61	12	-	36.5	24.5

Group **SF1** Species *S. fuscicollis* Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	17	6.8	20	14.6	4
2	10.3	18.8	22	17	3.5
3	27	27	13.4	22.5	4.5
Test	9.3	8	12.5	9.9	1.3
App					
1	160	42	9	70.3	45.8
2	9	3	2	4.7	2.2
3	6	5	4	5	0.6
Test	10	4	2	5.3	2.4
Tou					
1	314	64	15	131	92.6
2	-	4	3	3.5	0.5
3	18	7	5	10	4
Test	70	11	3	28	21.1

NF1	NF2	NF3	MEAN	St. e
8	13	7.8	9.6	1.7
1.8	5.5	6.3	4.5	1.4
3.8	4.5	3.8	4	0.2
1	1.3	3.3	1.9	0.7
10	69	3	27.3	20.9
5	10	3	6	2.1
2	6	2	3.3	1.3
2	10	18	10	4.6
22	82	9	37.7	22.5
11	25	18	18	4
8	8	4	6.7	1.3
4	13	66	27.7	19.3

	F/ NF1	F/ NF2	F/ NF3	MEAN	St. e
N					
1	10.5	15.3	9.8	11.9	1.7
2	5.3	9.5	10.8	8.5	1.7
3	3.8	3	3.8	3.5	0.3
Test	3.3	1.5	2.8	2.5	0.5
App					
1	3	5	26	11.3	7.4
2	17	3	6	8.7	4.3
3	3	11	31	15	8.3
Test	5	-	12	8.5	3.5
Tou					
1	4	6	47	19	14
2	21	4	7	10.7	5.2
3	4	13	35	17.3	9.2
Test	6	-	14	10	4

NF/ F1	NF/ F2	NF/ F3	MEAN	St. e
22.8	18.8	20.3	20.6	1.2
21.3	16.5	13.8	17.2	2.2
23.5	20.3	20.3	21.4	1.1
18	14.3	8	13.4	2.9
2	2	2	2	0
3	4	7	4.7	1.2
2	3	1	2	0.6
2	7	2	3.7	1.7
3	6	3	4	1
4	9	9	7.3	1.7
3	5	2	3.3	0.9
3	9	4	5.3	1.9

Group **SF2** Species *S. fuscicollis* Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	19.5	17.5	24	20.3	1.9
2	28.5	28.5	14.5	23.8	4.7
3	21.5	25.5	19.5	22.2	1.8
Test	12.5	15.5	9.5	12.5	1.7
App					
1	3	17	4	8	4.5
2	3	8	5	5.3	1.5
3	2	5	3	3.3	0.9
Test	2	6	2	3.3	1.3
Tou					
1	5	91	6	34	28.5
2	3	16	5	8	4
3	3	9	4	5.3	1.9
Test	3	8	3	4.7	1.7

NF1	NF2	NF3	MEAN	St. e
13	2.5	6	7.2	3.1
11	3.5	3	5.8	2.6
8.5	3.5	2	2.8	0.4
3	3.5	2	2.8	0.4
6	31	8	15	8
16	12	150	59.3	45.3
3	14	264	93.7	85.2
-	135	331	233	98
7	72	9	29.3	21.3
18	13	-	15.5	2.5
4	16	268	96	86.1
-	137	333	235	98

	F/ NF1	F/ NF2	F/ NF3	MEAN	St. e
N					
1	7	4	5.5	5.5	0.9
2	3.5	4.5	2	3.3	0.7
3	5	4	2	3.7	0.9
Test	1	3.5	0.5	1.7	0.9
App					
1	74	7	8	29.7	22.2
2	5	4	79	29.3	24.8
3	5	6	-	5.5	0.5
Test	4	28	-	16	12
Tou					
1	75	9	9	31	22
2	6	5	81	30.7	25.2
3	6	7	-	6.5	0.5
Test	4	33	-	18.5	14.5

NF/ F1	NF/ F2	NF/ F3	MEAN	St. e
19	22.5	13	18.2	2.8
18	18.5	17	17.8	0.4
15	22.5	20.5	19.3	2.2
15	10.5	7.5	11	2.2
5	8	9	7.3	1.2
9	4	11	8	2.1
3	3	7	4.3	1.3
4	7	4	5	1
5	9	10	8	1.5
10	5	15	10	2.9
4	4	8	5.3	1.3
4	8	5	5.7	1.2

Group **SF3**   Species *S. fuscicollis*   Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	30.5	17	14.5	20.7	5
2	14.5	16	14.5	15	0.5
3	15.5	8.5	19	14.3	3.1
Test	8.4	8	10	8.8	0.6
App					
1	6	7	10	7.7	1.2
2	5	8	5	6	1
3	8	5	7	6.7	0.9
Test	9	7	7	7.7	0.7
Tou					
1	9	8	10	9	0.6
2	6	11	6	7.7	1.7
3	10	6	8	8	1.1
Test	11	8	8	9	1

NF1	NF2	NF3	MEAN	St. e
5.5	2.5	5.5	4.5	1
8.5	9.5	4.5	7.5	1.5
2	3.5	5	3.5	0.9
2.5	3	2.5	2.7	0.2
32	183	17	77.3	53
35	60	38	44.3	7.9
-	132	11	71.5	60.5
-	45	505	275	230
161	184	18	121	51.9
38	62	42	47.3	7.4
-	133	14	73.5	59.5
-	46	506	275.5	229.5

	F/ NF1	F/ NF2	F/ NF3	MEAN	St. e
N					
1	10	6.5	4	6.8	1.7
2	5.5	2	0.5	2.7	1.5
3	4	1	0.5	1.8	1.1
Test	2	1	0	1	0.6
App					
1	19	8	15	14	3.2
2	67	28	-	47.5	19.5
3	7	31	69	35.7	18
Test	7	-	-	7	-
Tou					
1	21	11	17	16.3	2.9
2	70	34	-	52	18
3	8	31	75	38	19.7
Test	8	-	-	8	-

NF/ F1	NF/ F2	NF/ F3	MEAN	St. e
11	12.5	20	14.5	2.8
16.5	25.5	19.5	20.5	2.6
18	17	20	18.3	0.9
16.5	8	5.5	10	3.3
9	161	9	59.7	50.7
15	3	17	11.7	4.4
13	8	4	8.3	2.6
11	4	9	8	2.1
11	167	11	63	52
21	8	19	12.7	4.2
35	9	6	16.7	9.2
15	6	13	11.3	2.7

Group **SF5** Species *S. fuscicollis* Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	15.5	22.5	25	21	2.8
2	16.5	20	13	16.5	2
3	18.5	13.5	10	14	2.5
Test	12.5	14.5	6.5	11.2	2.4
App					
1	9	10	4	7.7	1.9
2	7	4	4	5	1
3	2	3	2	2.3	0.3
Test	4	3	4	3.7	0.3
Tou					
1	9	14	7	10	2.1
2	8	5	6	6.3	0.9
3	4	4	4	4	0
Test	5	4	7	5.3	0.9

NF1	NF2	NF3	MEAN	St. e
6	10	6	7.3	1.3
1.5	2.5	2.5	2.2	0.3
1	3	5	3	1.2
4	2	3.5	3.2	0.6
17	91	3	37	27.3
2	405	3	137.3	133.8
144	-	6	75	69
-	8	3	5.5	2.5
23	95	4	40.7	27.7
3	405	6	138	133.5
146	-	9	77.5	68.5
-	16	5	10.5	5.5

	F/ NF1	F/ NF2	F/ NF3	MEAN	St. e
N					
1	7	6	4	5.7	0.9
2	4	9	3.5	5.5	1.8
3	2.5	1.5	3.5	2.5	0.6
Test	3	2.5	2	2.5	0.3
App					
1	42	41	10	31	10.5
2	5	3	3	3.7	0.7
3	3	-	9	6	3
Test	12	63	12	29	17
Tou					
1	43	43	12	32.7	10.3
2	6	4	5	5	0.6
3	4	-	-	4	-
Test	13	64	25	34	15.4

NF/ F1	NF/ F2	NF/ F3	MEAN	St. e
9	10	4.5	7.8	1.7
23.5	24.5	13	20.3	3.7
18	12	16.5	15.5	1.8
10.5	7.5	11	9.7	1.1
47	62	2	37	18
3	3	6	4	1
12	9	3	8	2.6
5	9	1	5	2.3
59	64	3	42	19.6
4	4	7	5	1
16	12	5	11	3.2
7	11	2	6.7	2.6

Group **SF6** Species *S. fuscicollis* Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	12	15.5	16.5	14.7	1.4
2	20.5	10	15	15.2	3
3	13.5	14	16.5	14.7	0.9
Test	9.5	7.5	6	7.7	1
App					
1	5	3	5	4.3	0.7
2	5	3	4	4	0.6
3	23	10	5	12.7	2.9
Test	7	13	3	7.7	2.9
Tou					
1	6	4	9	6.3	1.5
2	5	5	5	5	0
3	24	11	8	14.3	4.9
Test	8	14	4	8.7	2.9

NF1	NF2	NF3	MEAN	St. e
3.5	4	6	4.5	0.8
7	4	4	5	1
5	0.5	5.5	3.7	1.6
4.5	1	1.5	2.3	1.1
12	55	35	34	12.4
28	431	35	164.7	133.2
76	-	350	213	137
-	-	11	11	-
14	57	36	35.7	12.4
201	436	38	225	115.5
228	-	353	290.5	62.5
-	-	13	13	-

	F/ NF1	F/ NF2	F/ NF3	MEAN	St. c
N					
1	3.5	2.5	2.5	2.8	0.3
2	2	2.5	2	2.2	0.2
3	2.5	1.5	0.5	1.5	0.6
Test	0.5	1	1	0.8	0.2
App					
1	17	13	11	13.7	1.8
2	9	79	-	44	35
3	24	38	-	31	7
Test	11	12	-	11.5	0.5
Tou					
1	21	15	14	16.7	2.2
2	41	81	-	61	20
3	31	39	-	35	4
Test	12	14	-	13	1

NF/ F1	NF/ F2	NF/ F3	MEAN	St. c
10	16	15.5	13.8	1.9
15	16	12.5	14.5	1
14	15	14.5	14.5	0.3
14	7	6.5	9.2	2.4
9	6	15	10	2.6
13	6	8	9	2.1
6	5	8	6.3	0.9
10	8	5	7.7	1.5
11	7	19	12.3	3.5
14	8	10	10.7	1.8
8	6	9	7.7	0.9
10	9	7	8.7	0.9

Group **SF8** Species *S. fuscicollis* Experiment 5.2 A

	F1	F2	F3	MEAN	St. e
N					
1	14.5	19	25.5	19.7	3.2
2	24	22.5	19	21.8	1.5
3	19.5	15	18	17.5	1.3
Test	9.5	8	9	8.8	0.4
App					
1	322	3	27	117.3	102.6
2	2	11	2	5	3
3	31	2	2	11.7	9.7
Test	46	9	6	20.3	12.9
Tou					
1	326	4	33	121	102.6
2	3	12	4	6.3	2.8
3	33	3	3	13	10
Test	47	11	8	22	12.5

NF1	NF2	NF3	MEAN	St. e
9.5	11	4.5	8.3	2
3.5	4	3	3.5	0.3
3	3.5	3	3.2	0.2
3	3.5	3	3.2	0.2
9	3	4	5.3	1.9
6	18	3	9	4.6
302	4	61	122.3	91.3
37	2	-	19.5	17.5
12	5	6	7.7	2.2
19	26	4	16.3	6.5
303	5	62	123.3	91.3
42	5	-	23.5	18.5

	F/ NF1	F/ NF2	F/ NF3	MEAN	St. c
N					
1	8.5	8.5	20	12.3	3.8
2	5	6	5.5	5.5	0.3
3	3.5	7.5	4	5	1.3
Test	5	2.5	2.5	3.3	0.8
App					
1	5	3	12	6.7	2.7
2	3	2	7	4	1.5
3	2	4	6	4	1.2
Test	2	3	4	3	0.6
Tou					
1	7	4	14	8.3	3
2	6	3	11	6.7	2.3
3	3	5	13	7	3.1
Test	3	4	5	4	0.6

NF/ F1	NF/ F2	NF/ F3	MEAN	St. c
18.5	22	16.5	19	1.6
20	30	13.5	21.2	4.8
23	18	18.5	19.8	1.6
10	12.5	12	11.5	0.8
6	7	5	6	0.6
3	4	13	6.7	3.2
3	3	7	4.3	1.3
1	6	2	3	1.5
7	8	7	7.3	0.3
5	6	15	8.7	3.2
4	4	9	5.7	1.7
3	11	5	6.3	2.4

Appendix 5 : Full results of experiment 5.2B, mixed-species trials.
Mixed Group **GP3** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e
N					
1	12.5	14.5	12.5	13.2	0.7
Test	6.5	3	8	5.8	1.5
App					
1	8	6	7	7	0.6
Test	4	8	5	5.7	1.2
Tou					
1	9	8	8	8.3	0.3
Test	4	9	6	6.3	1.5
	F/NF1	F/NF2	F/NF3	MEAN	St. e
N					
1	15.5	12	19.5	18.2	4.5
Test	4.5	5.5	6.5	4.5	1.3
App					
1	9	8	3	6.7	1.9
Test	4	5	3	4	0.6
Tou					
1	10	9	4	7.7	1.9
Test	5	6	4	5	0.6

NF1	NF2	NF3	MEAN	St. e
6.5	4.5	1.5	4.2	1.5
2.5	2	1	1.8	0.4
107	6	34	49	30.1
37	85	85	69	16
108	7	35	50	30.1
38	85	86	69.7	15.8
NF/F1	NF/F2	NF/F3	MEAN	St. e
11.5	10	11.5	3.5	0.8
4.5	6	7.5	1.8	1.0
8	9	6	7.7	0.9
1	16	42	19.7	12
9	11	8	9.3	0.9
2	17	43	20.7	12

Mixed Group **GP3** Species *S. fuscicollis*

	F1	F2	F3	MEAN	St. e
N					
1	15	27	12.5	18.2	4.5
Test	4	2.5	7	4.5	1.3
App					
1	21	71	6	32.7	19.7
Test	12	36	127	58.7	35.4
Tou					
1	22	79	7	36	21.9
Test	13	36	128	59	35.1
	F/NF1	F/NF2	F/NF3	MEAN	St. e
N					
1	17	19	22.5	19.5	1.6
Test	3.5	7	11.5	7.3	2.3
App					
1	2	4	4	3.3	0.7
Test	118	13	2	44.3	37
Tou					
1	3	5	4	4	0.6
Test	119	14	3	45.3	37

NF1	NF2	NF3	MEAN	St. e
2	4	4.5	3.5	0.8
3.5	2	0	1.8	1.0
274	23	16	104.3	84.9
24	23	-	23.5	0.5
274	24	17	105	84.5
25	24	-	24.5	0.5
NF/F1	NF/F2	NF/F3	MEAN	St. e
11	13	19	14.3	2.4
5.5	5	5	5.2	0.2
4	18	22	14.7	5.5
12	5	4	7	2.5
5	22	22	16.3	5.7
13	6	6	8.3	2.3

Key

N = Mean number of visits per individual. **App** = duration to initial approach. **Tou** = Duration to initial touch. **St. e** = Standard error.

Mixed Group **GP4** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e
N					
1	13.5	20	20	17.8	2.2
Test	9.5	3.5	6.5	6.5	1.7
App					
1	5	6	5	5.3	0.3
Test	16	30	7	17.7	6.7
Tou					
1	6	7	7	6.7	0.3
Test	17	32	8	19	7
	F/NF1	F/NF2	F/NF3	MEAN	St. e
N					
1	19.5	16.5	23.5	19.8	2.1
Test	6	7.5	8.5	7.3	0.7
App					
1	4	3	4	3.7	0.3
Test	5	4	6	5	0.6
Tou					
1	5	4	5	4.7	0.3
Test	6	5	7	6	0.6

NF1	NF2	NF3	MEAN	St. e
3	4.5	1.5	3	0.9
1	1.5	2	1.5	0.3
14	187	260	153.7	73
-	-	15	15	
18	188	261	155.7	72
-	-	16	16	
NF/F1	NF/F2	NF/F3	MEAN	St. e
16	13	11.5	13.5	1.3
8.5	5	7	6.8	1.0
2	15	3	6.7	4.2
4	19	13	12	4.4
2	16	3	7	4.5
5	20	13	12.7	4.3

Mixed Group **GP4** Species *S. fuscicollis*

	F1	F2	F3	MEAN	St. e
N					
1	14.5	15.5	19	16.3	1.4
Test	5.5	3	7	5.2	1.2
App					
1	4	32	5	13.7	9.2
Test	37	2	4	14.3	11.3
Tou					
1	5	33	7	15	9
Test	38	3	5	15.3	11.3
	F/NF1	F/NF2	F/NF3	MEAN	St. e
N					
1	12.5	16	10	12.8	1.7
Test	10	10.5	6	8.8	1.4
App					
1	60	16	12	29.3	15.4
Test	14	26	3	14.3	6.6
Tou					
1	60	17	13	30	15
Test	16	27	4	15.7	6.6

NF1	NF2	NF3	MEAN	St. e
0.5	3	1.5	1.7	0.7
0.5	6.5	5	4	1.8
-	93	18	55.2	37.5
-	142	22	82	60
-	94	19	56.5	37.5
-	143	23	83	60
NF/F1	NF/F2	NF/F3	MEAN	St. e
8.5	8.5	15	10.7	2.2
9.5	7	6	7.5	1.0
5	3	14	7.3	3.4
56	3	4	21	17.5
5	5	14	8	3
57	4	5	22	17.5

Key

N = Mean number of visits per individual. **App** = duration to initial approach. **Tou** = Duration to initial touch. **St. e** = Standard error.

Mixed Group **GP6** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e
N					
1	13.5	16	8.5	12.7	2.2
Test	9	8	9	8.7	0.3
App					
1	4	26	3	11	7.5
Test	8	5	4	5.7	1.2
Tou					
1	4	32	4	13.3	9.3
Test	9	6	5	6.7	1.2
	F/NF1	F/NF2	F/NF3	MEAN	St. e
N					
1	7	13	17	12.3	2.9
Test	5	6	9	6.7	1.2
App					
1	3	2	2	2.3	0.3
Test	8	1	3	4	2.1
Tou					
1	4	3	3	3.3	0.3
Test	9	2	4	5	2.1

NF1	NF2	NF3	MEAN	St. e
6.5	5.5	5.5	5.8	0.3
3	2.5	2.5	2.7	0.2
223	8	9	80	71.5
5	82	242	109.7	69.8
224	9	10	81	71.5
7	83	243	111	69.6
NF/F1	NF/F2	NF/F3	MEAN	St. e
13.5	15	26	18.2	3.9
7.5	8.5	9	8.3	0.4
3	8	2	4.3	1.9
10	3	2	5	2.5
4	9	3	5.3	1.9
11	4	3	6	2.5

Mixed Group **GP6** Species *S. fuscicollis*

	F1	F2	F3	MEAN	St. e
N					
1	11.5	12.5	13	12.3	0.4
Test	3	2	4	3	0.6
App					
1	15	5	5	8.3	3.3
Test	29	17	35	27	5.3
Tou					
1	19	6	5	10	4.5
Test	32	29	36	32.3	2.0
	F/NF1	F/NF2	F/NF3	MEAN	St. e
N					
1	12	12	21.5	15.2	3.2
Test	11	6	2.5	6.5	2.5
App					
1	26	20	60	35.3	12.5
Test	11	56	-	33.5	22.5
Tou					
1	26	21	61	36	12.6
Test	12	57	-	34.5	22.5

NF1	NF2	NF3	MEAN	St. e
2	4	1	2.3	0.9
1	2	0.5	1.2	0.4
-	27	317	172	145
-	236	-	236	
-	28	319	173.5	145.5
-	237	-	237	
NF/F1	NF/F2	NF/F3	MEAN	St. e
8	11	15	11.3	2.0
5.5	6.5	4.5	5.5	0.6
87	37	3	42.3	24.4
4	121	101	75.3	36.1
88	38	4	43.3	24.4
5	122	102	76.3	26.1

Key

N = Mean number of visits per individual. **App** = duration to initial approach. **Tou** = Duration to initial touch. **St. e** = Standard error.

Mixed Group **GP7** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e
N					
1	19.5	22	13.5	18.3	2.5
Test	16	2.5	4.5	7.7	4.2
App					
1	5	8	4	5.7	1.2
Test	11	3	2	5.3	2.8
Tou					
1	8	10	4	7.3	1.8
Test	12	4	3	6.3	2.8
	F/NF1	F/NF2	F/NF3	MEAN	St. e
N					
1	10.5	7.5	7.5	8.5	1
Test	6	8.5	8	7.5	0.8
App					
1	15	3	4	7.3	3.8
Test	5	4	5	4.7	0.3
Tou					
1	16	4	5	8.3	3.8
Test	6	5	6	5.7	0.3

NF1	NF2	NF3	MEAN	St. e
3	3	5	3.7	0.7
3	3	1.5	2.5	0.5
4	5	29	12.7	8.2
14	5	46	21.7	12.4
5	6	30	13.7	8.2
15	6	47	22.7	12.4
NF/F1	NF/F2	NF/F3	MEAN	St. e
8	10.5	9.5	9.3	0.7
5.5	3.5	5	4.7	0.6
4	27	3	11.3	7.8
2	2	2	2	
5	28	4	12.3	7.8
3	3	3	3	

Mixed Group **GP7** Species *S. fuscicollis*

	F1	F2	F3	MEAN	St. e
N					
1	18.5	25	29	24.2	3.1
Test	4.5	9.5	6	6.7	1.5
App					
1	31	45	232	102.7	64.8
Test	83	25	58	55.3	16.8
Tou					
1	32	48	232	104	64.2
Test	84	26	59	56.3	16.8
	F/NF1	F/NF2	F/NF3	MEAN	St. e
N					
1	14.5	15	7.5	12.3	2.4
Test	4.5	5	5	4.8	0.2
App					
1	35	122	185	114	43.5
Test	77	18	103	66	25.1
Tou					
1	36	122	186	114.7	43.5
Test	81	19	104	68	25.4

NF1	NF2	NF3	MEAN	St. e
3.5	11	9	7.8	2.2
6.5	4.5	2	4.3	1.3
70	53	42	55	8.1
86	88	274	149.3	62.3
71	54	43	56	8.1
87	89	274	150	62
NF/F1	NF/F2	NF/F3	MEAN	St. e
9	14.5	15.5	13.0	2.0
8.5	6	6.5	7	0.8
134	37	31	67.3	33.4
53	75	87	71.7	10
134	8	31	57.7	38.7
54	76	88	72.7	10

Key

N = Mean number of visits per individual. **App** = duration to initial approach. **Tou** = Duration to initial touch. **St. e** = Standard error.

Mixed Group **GP8** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e	NF1	NF2	NF3	MEAN	St. e
N										
1	17.5	13	13	14.5	1.5	6	8	3	5.7	1.5
Test	6.5	8.5	7.5	7.5	0.6	0.5	2.5	3.5	2.2	0.9
App										
1	6	3	6	5	1	13	7	5	8.3	2.4
Test	8	4	4	5.3	1.3	9	77	5	30.3	23.4
Tou										
1	7	5	7	6.3	0.7	14	8	6	9.3	2.4
Test	9	5	5	6.3	1.3	10	78	7	31.7	23.2
	F/NF1	F/NF2	F/NF3	MEAN	St. e	NF/F1	NF/F2	NF/F3	MEAN	St. e
N										
1	14	11.5	15.5	13.7	1.2	15.5	10	9	11.5	2.0
Test	4.5	8	6	6.2	1.0	6.5	13	10	9.8	1.9
App										
1	6	4	3	4.3	0.9	12	7	6	8.3	1.9
Test	3	4	20	9	5.5	5	6	3	4.7	0.9
Tou										
1	6	5	4	5	0.6	13	8	8	9.7	1.7
Test	4	5	21	10	5.5	6	8	4	6	1.2

Mixed Group **GP8** Species *S. fuscicollis*

	F1	F2	F3	MEAN	St. e	NF1	NF2	NF3	MEAN	St. e
N										
1	15	12	13	13.3	0.9	2.5	3.5	2	2.7	0.4
Test	6.5	3.5	7.5	5.8	1.2	4	5	1.5	3.5	1.0
App										
1	3	5	37	15	11	26	40	44	36.7	5.5
Test	5	17	8	10	3.6	5	222	-	113.5	108.5
Tou										
1	4	6	37	15.7	10.7	27	68	45	46.7	11.9
Test	6	18	9	11	3.6	6	225	-	115.5	109.5
	F/NF1	F/NF2	F/NF3	MEAN	St. e	NF/F1	NF/F2	NF/F3	MEAN	St. e
N										
1	21	13	27.5	20.5	4.2	8.5	15	17	13.5	2.6
Test	10.5	8.5	3.5	7.5	2.1	5	11.5	5	7.2	2.2
App										
1	3	14	36	17.7	9.7	4	60	4	22.7	18.7
Test	8	13	-	10.5	2.5	4	6	14	8	3.1
Tou										
1	5	15	36	18.7	9.1	5	60	5	23.3	18.3
Test	9	14	-	11.5	2.5	5	10	15	10	2.9

Key
N = Mean number of visits per individual. **App** = duration to initial approach. **Tou** = Duration to initial touch. **St. e** = Standard error.

Appendix 6 : New food and non-food objects for Experiment 5.2C. Scores for all trials presented to mixed-species groups.

Mixed Group **GP3** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e
N					
1	19	13.5	14	15.5	1.8
Test	8	6.5	6.5	7	0.5
App					
1	3	7	4	4.7	1.2
Test	4	7	6	5.7	0.9
Tou					
1	4	8	5	5.7	1.2
Test	6	8	8	7.3	0.7

NF1	NF2	NF3	MEAN	St. e
5	3.5	9	5.8	1.6
1	1.5	4	2.2	0.9
5	5	5	5	0
98	-	4	51	47
6	6	6	6	0
99	-	5	52	47

Mixed Group **GP3** Species *S. fuscicollis*

	F1	F2	F3	MEAN	St. e
N					
1	18	17.5	17.5	17.7	0.2
Test	8	7	8	7.7	0.3
App					
1	4	4	3	3.7	0.3
Test	6	4	4	4.7	0.7
Tou					
1	5	5	4	4.7	0.3
Test	8	5	5	6	1

NF1	NF2	NF3	MEAN	St. e
6	6	8	6.7	0.7
2.5	2.5	3	2.7	0.2
42	3	3	16	13
11	6	9	8.7	1.5
43	4	4	17	13
12	7	10	9.7	1.5

Key N = Mean number of visits per individual. **App** = duration to initial approach. **Tou** = Duration to initial touch. **St. e** = Standard error.

Mixed Group **GP4** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e	NF1	NF2	NF3	MEAN	St. e
N										
1	12	13	14.5	13.2	0.7	6	8	9.5	7.8	1.0
Test	9	7	6.5	7.5	0.8	3	1.5	1.5	2	0.5
App										
1	3	3	3	3	0	2	5	3	3.3	0.9
Test	11	2	14	9	3.6	106	141	9	85.3	39.5
Tou										
1	4	4	4	4	0	3	6	4	4.3	0.9
Test	12	3	13	9.3	3.2	107	142	10	86.3	39.5

Mixed Group **GP4** Species *S. fuscicollis*

	F1	F2	F3	MEAN	St. e	NF1	NF2	NF3	MEAN	St. e
N										
1	17.5	13.5	17.5	16.2	1.3	6.5	5.5	7	6.3	0.4
Test	5	7	6.5	6.2	0.6	3.5	4	4.5	4	0.3
App										
1	3	5	2	3.3	0.9	8	3	1	4	2.1
Test	61	5	3	23	19	2	12	4	6	3.1
Tou										
1	4	6	8	6	1.2	9	4	2	5	2.1
Test	62	6	4	24	19	3	13	5	7	3.1

Mixed Group **GP6** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e	NF1	NF2	NF3	MEAN	St. e
N										
1	9.5	18.5	16	14.7	2.7	13	9	7.5	9.8	1.6
Test	10.5	12	8	10.2	1.2	3	4	3.5	3.5	0.3
App										
1	2	3	7	4	1.5	4	7	4	5	1
Test	3	4	4	3.7	0.3	4	19	4	9	5
Tou										
1	3	4	8	5	1.5	5	8	5	6	1
Test	4	5	5	4.7	0.3	5	20	5	10	5

Mixed Group **GP6** Species *S. fuscicollis*

	F1	F2	F3	MEAN	St. e	NF1	NF2	NF3	MEAN	St. e
N										
1	12.5	14	17.5	14.3	1.5	5	6	9	6.7	1.2
Test	6.5	6.5	7	6.7	0.2	2.5	4	1	2.5	0.9
App										
1	6	6	4	5.3	0.7	36	84	2	40.7	23.8
Test	9	122	31	54	34.6	27	-	5	16	11
Tou										
1	7	7	5	6.3	0.7	37	86	3	42	24.1
Test	10	123	33	55.3	34.5	28	-	6	17	11

Mixed Group **GP7** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e	NF1	NF2	NF3	MEAN	St. e
N										
1	11	18.5	16	15.2	2.2	5	5.5	3.5	4.7	0.6
Test	7	12	8	9	1.5	3	2	2.5	2.5	0.3
App										
1	4	3	7	4.7	1.2	4	2	2	2.7	0.7
Test	8	4	4	5.3	1.3	3	7	4	4.7	1.2
Tou										
1	5	4	8	5.7	1.2	5	3	3	3.7	0.7
Test	9	5	5	6.3	1.3	4	8	5	5.7	1.2

Mixed Group **GP7** Species *S. fuscicollis*

	F1	F2	F3	MEAN	St. e	NF1	NF2	NF3	MEAN	St. e
N										
1	12	11	15.5	12.8	1.4	8	5.5	4	5.8	1.2
Test	6	6.5	6.5	6.3	0.2	1	2	1.5	1.5	0.3
App										
1	23	66	207	98.7	55.6	52	121	126	99.7	23.9
Test	76	47	48	57	9.5	46	247	-	146.5	100.5
Tou										
1	24	67	208	99.7	55.6	52	122	127	100.3	24.2
Test	76	48	49	57.7	9.2	47	248	-	147.5	100.5

Mixed Group **GP8** Species *S. labiatus*

	F1	F2	F3	MEAN	St. e
N					
1	10	17	14.5	13.8	2.1
Test	10.5	8.5	7.5	8.8	0.9
App					
1	2	14	5	7	3.6
Test	4	22	3	9.7	6.2
Tou					
1	3	16	4	7.7	4.2
Test	5	23	4	10.7	6.2

NF1	NF2	NF3	MEAN	St. e
9.5	7.5	6	7.7	1.0
3.5	5	2.5	3.7	0.7
5	4	14	7.7	3.2
6	13	4	7.7	2.7
6	5	15	8.7	3.2
7	14	5	8.7	2.7

Mixed Group **GP8** Species *S. fuscicollis*

	F1	F2	F3	MEAN	St. e
N					
1	14.5	13	23.5	17	3.3
Test	6.5	5	8	6.5	0.9
App					
1	3	6	3	4	1
Test	3	16	5	8	4.0
Tou					
1	4	7	4	5	1
Test	4	17	6	9	4.0

NF1	NF2	NF3	MEAN	St. e
9	13.5	5.5	9.3	2.3
1.5	3	3.5	2.7	0.6
3	72	27	34	20.2
13	7	431	150.3	140.3
4	73	28	35	20.2
14	8	431	151	140