Social Learning in Mixed-Species Troops of *Saguinus fuscicollis* and *Saguinus labiatus*: Tests of Foraging Benefit Hypotheses in Captivity

MARK JOHN PRESCOTT

University of Stirling

Thesis submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

May 1999

06/00

Contents

Chapter 1 Tamarin Mixed-Species Associations: An Introduction

Chapter 2 Costs and Benefits of Tamarin Mixed-Species Associations

Chapter 3 Foraging and Learning

Chapter 4 Studying Captive Tamarin Troops at Belfast Zoological Gardens

Chapter 5 Social Learning About Food Acquisition

Chapter 6 Social Learning About Food Palatability

Chapter 7 Divergence in Forest Utilisation in Wild Mixed-Species Troops of *S. fuscicollis* and *S. labiatus*

Chapter 8 Foraging Height Preferences and Inter-specific Feeding Competition in Captivity

Chapter 9 Social Learning About Food Location

Chapter 10 Social Learning About Food Patch Quality

Chapter 11 General Discussion

Acknowledgements

I would like here to express my appreciation and gratitude to the many individuals and organisations without which I could not have completed this body of work. First and foremost, I would like to thank Dr. Hannah Buchanan-Smith for her unflagging support and supervision throughout this thesis. From its conception through to its completion, I received all the conscientious guidance, constructive criticism, encouragement, council and friendship I wished for, no matter how busy she herself was. I must thank her also for assistance outside of the thesis: for career guidance, for the opportunity to conduct more fieldwork and to teach, for encouraging me to present at conferences, for the Research Assistantship, and for ferrying me to and from Belfast!

Secondly, I wish to thank Dr. Scott Hardie whose friendship, honest advice, frank discussion, foresight and willing support have been invaluable throughout this thesis. I am also particularly grateful for his setting-up and initiating of the research at Belfast Zoological Gardens, and for the generous opportunity to join the research expedition in Bolivia in 1997. I am profoundly indebted to these two people and, again, I offer them my deepest thanks. From them I have learned a great deal and have had a lot of fun doing so.

A great many thanks go out to the Belfast Parks Department and Belfast Zoological Gardens for allowing the study to take place, for the use of the office and resources, and for the numerous other forms of assistance freely provided during my time in Belfast. All the zoo staff extended their absolute friendship, co-operation and aid during my summers at the zoo. In particular, I would like to acknowledge John Stronge (Zoo Manager) and Mark Challis (Assistant Zoo Manager) who were always helpful and receptive to my requests. Thanks to the keepers, especially Paul Allen, Mark Rossi, Julia Coulter, Alyn Cairns and Kirsten Stites for looking after the animals and/or allowing me to interrupt their schedule, whether it be to catch and re-locate animals, to procure mealworms, or for testing. Thanks also to the technical services staff for customising existing enclosures and to the administrative staff, Patricia, Imelda, Evelyn and Kathleen. I often wondered what on earth these people at the zoo thought of me spending all day of nearly every day staring at monkeys.

The research was funded by a University of Stirling Studentship and for that I am exceedingly grateful. I must also thank the University for financial assistance in attending conferences in Britain and abroad. Thanks are owed to Dr. Jim Anderson, my second supervisor, for use of his extensive reprint collection, for help with obscure references and for the job tip-offs. Thanks also to all the technical and administrative staff at Stirling, especially Bob Lavery and Bruce Sutherland, for their reliable and superbly executed assistance.

I am grateful to Prof. Bob Elwood for generously securing the position as Research Associate at The Queens University of Belfast. Without the vital use of the facilities there this thesis would have taken much longer to complete.

Grazie mille to my Italian colleagues, Armelle Queyras and Augusto Vitale, for their generous idea for Chapter 6, and muchas gracias to Garoto Nascimento, my guide in the Pando Department, Bolivia. His skill and hard work in locating, identifying and tracking the tamarins there played an absolutely vital role in the fieldwork data collection. I must thank, also, all the people of the Pando who offered their kind hospitality. I have great respect for the people who live and work alongside the tamarins in the wonderful place that is the rain forest.

I am extremely grateful to my parents for their tremendous encouragement and support, both emotionally and financially, throughout my time at Stirling. The laptop computer, the equipment Dad made, the loans, the proof reading, and the 'ear' during the lengthy phone calls when all wasn't going well, were all essential contributions.

Last, but by no means least, thanks to all my friends and colleagues at Stirling for their interest, encouragement, friendship and good humour, especially Jayne Morris, Donald Morrison, Roisin Ash, Sissy Karakitsou, Marion Murray and Vicky Perry. Without you this would have been a much harder task.

This thesis is dedicated to my grandfather, Stephen Dulcamara, who fostered in me a sense of the scientific at an early age.

Publications and Conference Presentations

The following publications and conference presentations have been adapted from experimental work detailed in this thesis:

Prescott, M.J., & Buchanan-Smith, H.M. (accepted). Intra- and inter-specific social learning of a novel food task in two species of tamarin. *International Journal of Comparative Psychology.*

Prescott, M.J., & Buchanan-Smith, H.M. (1999). *Foraging efficiency in single- and mixed-species troops of tamarins.* Abstract published in the proceedings of the PSGB Spring Meeting, Liverpool, England, U.K.

Prescott, M.J., & Buchanan-Smith, H.M. (1998). *Does the presence of a congener affect foraging efficiency in mixed-species tamarin troops?* Abstract published in the proceedings of the XVIIth IPS Congress, Antananarivo, Madagascar.

Prescott, M.J., & Buchanan-Smith, H.M. (1998). *Vertical segregation and inter-specific competition in mixed-species tamarin troops.* Abstract published in the proceedings of the PSGB Spring Meeting, Bristol, England, U.K.

Prescott, M.J., & Buchanan-Smith, H.M. (1997). *Intra- and inter-specific stimulus enhancement in two-species of tamarin.* Abstract published in the proceedings of the ASAB Summer Meeting, St. Andrews, Scotland, U.K.

Prescott, M.J., & Buchanan-Smith, H.M. (1997). *Feeding height preferences in single and mixed-species tamarin troops.* Abstract published in the proceedings of the SCAB Winter Meeting, St. Andrews, Scotland, U.K.

Prescott, M.J., Buchanan-Smith, H.M., & Hardie, S.M. (1999). *The role of Belfast Zoo in understanding the function of tamarin mixed-species troops.* Abstract published in the proceedings of the British and Irish Federation of Zoos Research Group Symposium on Zoo Research, Paignton Zoo Environmental Park, England, U.K.

Buchanan-Smith, H.M., Caceres, C., Hardie, S.M., & Prescott, M.J. (submitted). Distribution and forest utilisation of *Saguinus* and other primates of the Pando Department, Northern Bolivia. *International Journal of Primatology.*

Buchanan-Smith, H.M., & Prescott, M.J. (1998). *Interspecific influences in response to novelty.* Abstract published in the proceedings of the XVIIth IPS Congress, Antananarivo, Madagascar.

Buchanan-Smith, H.M., Hardie, S.M., Prescott, M.J., Stronge, J., & Challis, M. (1996). Callitrichids at Belfast Zoological Gardens, Northern Ireland. *Neotropical Primates, 4,* 143-146.

Hardie, S.M., Buchanan-Smith, H.M., & Prescott, M.J. (1998). *Unravelling the behaviour of mixed-species tamarin groups: The role of Belfast Zoo.* Abstract published in the proceedings of the PSGB Winter Meeting, London, England, U.K.

Abstract

The selective costs and benefits affecting the evolution of group living have long interested behavioural ecologists because knowledge of these selective forces can enhance our understanding not only of why organisms live in groups, but also why species exhibit particular patterns of social organisation. Tamarins form stable and permanent mixed-species troops providing an excellent model for examining the costs and benefits hypothesised for group living. However, testing hypotheses in the wild is difficult, not least because participating species are rarely found out of association. In contrast, in captivity it is possible to compare matched single- and mixed-species troops and also to study the same individuals in single- and mixed-species troops to see what effect the presence of a congener has on behaviour. In this way, captive work can help us confirm, reject, or refine the hypotheses, and aids in the generation of new ones, for relating back to the wild. The utility of this approach is demonstrated in this thesis which explored some of the foraging benefit hypotheses and, in particular, the underlying notion that individuals in tamarin mixed-species troops can increase their foraging efficiency through social learning. Single- and mixed-species troops of *Saguinus fuscicollis* and *S. labiatus* were studied at Belfast Zoological Gardens. It was found that social interaction with conspecifics and congeners facilitated learning by individuals of various types of food-related information (food palatability, location, and method of access). However, although social learning operated in mixed-species troops, it did so under the shadow of inter-specific dominance. The results were used, in conjunction with field observations in Bolivia, to make inferences about the adaptive function of social learning in the wild. These findings strengthen the hypotheses which suggest that increased opportunity for social learning, through an increase in troop

size and as a result of species divergence in behaviour, is an adaptive advantage of mixed-species troop formation in tamarins.

List of Colour Plates

Chapter 1

Tamarin Mixed-Species Associations: An Introduction

As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into contact with each other, than between the species of distinct genera.

[Darwin, 1892: p. 55]

1.1 Introduction

Polyspecific associations, where two or more species aggregate in a non-random manner, have been reported in a number of animal taxa, including spiders (e.g., Hodge & Uetz, 1992, 1996), fish (e.g., Ehrlich & Ehrlich, 1973; Itzkovitz, 1977; Wolf, 1985; Allen, 1986; Debrot & Myrberg, 1988; Sakia & Kohda, 1995), birds (e.g., Moynihan, 1962; Morse, 1970; Munn & Terborgh, 1980; Powell, 1989; Mahon *et al.*, 1992; Eguchi *et al.*, 1993; Graves & Gotelli, 1993; Latta & Wunderle, 1996) and mammals (e.g., chiroptera: Bradbury, 1975; cetacea: Pilleri & Knuckley, 1969; artiodactyla: Leuthold, 1977; Gosling, 1980; Sinclair, 1985; Fitzgibbon, 1990; and primates: summarised in Cords, 1987). Amongst the primates, such associations occur principally in the arboreal, diurnal African cercopithecines and Amazonian callitrichines (e.g., Terborgh, 1983; Gautier-Hion, 1988) and range in duration and stability from ephemeral aggregations in feeding trees (e.g., Gautier & Gautier-Hion, 1969; Gartlan & Struhsaker, 1972; Struhsaker, 1975; Oates & Whitesides, 1980; Waser, 1982; Whitesides, 1989), to relatively permanent closed-membership troops (e.g., Gautier-Hion & Gautier, 1974; Gautier-Hion *et al.*, 1983; Terborgh, 1983; Buchanan-Smith, 1990a; Peres, 1992a,b). Along this continuum, the associations formed between sympatric tamarin troops (genus *Saguinus*) in western lowland Amazonia are among the most permanent and cohesive and are noted for their stability. For example, Terborgh (1983) reports one mixed-species troop of *S. fuscicollis* (saddle-backed tamarin) and *S. imperator* (emperor tamarin) associating for at least three years; and mixed-species troops of *S. fuscicollis* and *S. mystax* (moustached tamarin) have been reported to spend between 72 % and 98 % of their daily activity period together (Garber, 1988b; Heymann, 1990a; Peres, 1992b; Smith, 1997) (see Table 1.1: Note that each study has its own definition of 'in association').

Mixed-species tamarin troops are invariably formed between *S. fuscicollis* with either one of the three species of the *S. mystax* group (Hershkovitz, 1977) with which it is sympatric. These are *S. mystax* (Castro & Soini, 1978; Ramirez, 1984; Norconk, 1985; Garber, 1986, 1988a,b; Garber & Teaford, 1986; Heymann & Sicchar-Valdez, 1988; Heymann, 1990a; Peres, 1992a,b, 1993a,b), *S. labiatus* (red-bellied tamarin) (Yoneda, 1981, 1984a; Pook & Pook, 1982; Buchanan-Smith, 1990a; Hardie, 1998), and *S. imperator* (Terborgh, 1983; Buchanan-Smith, 1999). The species of the *S. mystax* group are considered either mostly or completely allopatric with each other (although detailed geographical data are lacking) (Hershkovitz, 1977; Hershkovitz, 1982; Rylands *et al.*, 1993) and it has been reported that, in western Pando, Bolivia, where *S. mystax* and *S. labiatus* are sympatric, they do not associate (Izawa & Bejarano, 1981). However, it should be noted that a recent expedition to the Pando failed to confirm this sympatry (Buchanan-Smith, unpubl. obs.).

Table 1.1: Reported time spent in inter-specific association for associated tamarin species (adapted from Heymann & Buchanan-Smith, submitted).

Associating	**Species**	**D**[1]	**T**[2]	**Reference**
S. mystax mystax	*S. fuscicollis nigrifrons*	20	72	Garber, 1988b
		20	82	Heymann, 1990a
		50	83	Smith, 1997
S. mystax pileatus	*S. fuscicollis avilapiresi*	50	98	Peres, 1992b
S. labiatus labiatus	*S. fuscicollis weddelli*	?	43 - 47	Pook & Pook, 1982
		50	83	Buchanan-Smith, 1990a
		25	50 - 70	Buchanan-Smith, unpubl. data
S. imperator subgrisescens	*S. fuscicollis weddelli*	25	19	Windfelder, 1997
Callimico goeldii	*S. fuscicollis weddelli*	?	30	Pook & Pook, 1982
	S. labiatus labiatus	?	3	Pook & Pook, 1982
	S. fuscicollis weddelli + *S. labiatus labiatus*	?	44	Pook & Pook, 1982

[1] D: distance criterion (metres).

[2] T: % of active time spent in association.

There are twelve subspecies of *S. fuscicollis* and two of *S. labiatus*. The geographical distribution of *S. fuscicollis weddelli* (Weddell's saddle-backed tamarin) (Plate 1) is the widest of all subspecies of *S. fuscicollis* and overlaps that of *S. labiatus labiatus* (red-bellied tamarin or Geoffroy's moustached tamarin) (Plate 2) in parts of Bolivia, Brazil and Peru (Rylands *et al.*, 1993). This thesis examines the adaptive significance of the mixed-species troops formed between these two particular subspecies.

Numerous hypotheses have been proposed concerning the adaptive advantages promoting mixed-species troops in tamarins (see Heymann & Buchanan-Smith, submitted). These are not fundamentally different from those explaining the evolution of intra-specific gregariousness in animals in general (e.g., Bertram, 1978), except that kin-based gains accrued to genetically related individuals (Hamilton, 1964) cannot be involved. However, this need not preclude unrelated individuals, even of another species, from secondarily taking advantage of traits previously fixed in kin-based groups (e.g., early warning of predators by sentinel individuals: Sherman, 1977). It has been suggested that associating tamarin species benefit from one another by increasing their foraging efficiency, their resource-defence potential, or by decreasing their risk of attack by predators (e.g., Terborgh, 1983; Garber, 1988b, 1993a; Buchanan-Smith, 1990a; Norconk, 1990b; Peres, 1992a,b, 1993a, 1996). This thesis is primarily concerned with the first group of hypotheses, the foraging benefit hypotheses, implicit in many of which is the notion of inter-specific information transfer through social learning (i.e., learning from others or having one's learning influenced by others). Consequently, social learning is a central theme in this thesis and experimental investigations of the foraging benefits hypotheses that involve social learning feature highly. Given this focus, the first chapter in

Plate 1: *S. fuscicollis weddelli* (Weddell's saddle-backed tamarin).

Plate 2: *S. labiatus labiatus* (red-bellied tamarin or Geoffroy's moustached tamarin).

this thesis is a review of the general behaviour and ecology of tamarins and the second is a review of the hypotheses proposed for animal associations in general and tamarin mixed-species troops in particular. The third chapter discusses learning during foraging and includes a section exploring the adaptivity of social learning (i.e., how individuals may increase their inclusive fitness by social learning). Also included in this chapter is a justification for expecting social learning to operate in wild mixed-species troops. Following this is the final introductory chapter, detailing the utility and methodology of studying tamarin mixed-species troops in captivity. I then turn to experimental and observational studies of captive and wild tamarins. The studies in Chapters 5, 6, 9 and 10 explore whether social learning concerning various aspects of food can occur between species in captive mixed-species troops, whether it is plausible that learning of this kind also operates in wild mixed-species troops, how it might be adaptive in these, and what types of social learning process are likely to be involved. Chapter 7 presents data collected in the Pando Department of north-western Bolivia to examine the role species differences in behaviour and ecology have in permitting co-existence in mixed-species troops. This is followed by a chapter which details a study exploring feeding height preferences and inter-specific feeding competition in captivity. The final chapter (Chapter 11) gathers the available evidence for social learning and species divergence in behaviour as advantages of mixed-species tamarin troops and discusses them in terms of the specific and overall costs and benefits to participants in these troops. Limitations of the studies in the thesis and recommendations for improvement are also highlighted in this chapter and suggestions for future research are given. For the benefit of the reader, an appendix giving the common (English) names of all species mentioned in the text is provided on page 446.

1.2 Tamarin Behaviour and Ecology

This section attempts to provide an overview of the behaviour and ecology of the tamarins as presently understood. Any such overview necessitates some generalisation between species. Inter-specific differences do occur within the genus, however, and where pertinent these are indicated in the text.

1.2.1 Phylogeny and Systematics

Tamarins of the genus *Saguinus* are small-bodied (300 - 550g: Napier & Napier, 1967; Hershkovitz, 1977), diurnal, arboreal, South American primates, belonging to the infraorder Platyrrhini (New World monkeys). The platyrrhine monkeys are believed to have evolved from separate prosimian linneages to those of the apes and catarrhine (Old World) monkeys of Africa following restriction to the American subtropics in the late Oligocene (Fleagle, 1988). Within the Platyrrhini, the phylogeny and systematics of the tamarins is currently subject to debate, even at the family level (Rylands *et al.*, 1993). In this thesis, they are considered as belonging to the subfamily Callitrichinae of the family Cebidae, after Rosenberger (1981) and Schneider *et al.* (1993)[1]. The other callitrichine genera include *Leontopithecus* (lion-tamarins), *Callithrix* (marmosets), *Cebuella* (pygmy marmoset), and *Callimico* (Goeldi's monkey)[2] (see Table 1.2).

---

[1] The main alternative is to consider them as part of the family Callitrichidae after the seminal work of Hershkovitz, 1977.

[2] The enigmatic *Callimico* is either included in the subfamily Callitrichinae (e.g., Rosenberger, 1981), is assigned to the subfamily Callimiconinae (Thorington, 1976), or is given its own family, the Callimiconidae (e.g., Hershkovitz, 1977).

Table 1.2: Taxonomy of the subfamily Callitrichinae (Rosenberger, 1981) (genera and common names after Hershkovitz, 1977; species as listed in Rylands, 1995).

Subfamily	**Genus**	**Species (Common Name)**
Callitrichinae		
	Cebuella	*C. pygmaea* (pygmy marmoset)
	Callithrix	*C. argentata* (silvery/bare-ear marmoset)
		C. leucippe (golden-white bar-ear marmoset)
		C. melanura (black-tailed marmoset)
		C. intermedia (Aripuana marmoset)
		C. emiliae (Snethalge's marmoset)
		C. nigriceps (black-headed marmoset)
		C. marcai (Marca's marmoset)
		C. humeralifer (black and white tassel-ear marmoset)
		C. chysoleuca (golden-white tassel-ear marmoset)
		C. mauesi (Maues marmoset)
		C. saterei (Satere marmoset)
		C. jacchus (common/white tufted-ear marmoset)
		C. pencilliata (black tufted-ear marmoset)
		C. kuhli (Wied's black-tufted-ear marmoset)
		C. geoffroyi (Geoffroy's tufted-ear marmoset)
		C. aurita (buffy tufted-ear marmoset)
		C. flaviceps (buffy-headed marmoset)
	Saguinus	*S. mystax* (moustached tamarin)
		S. labiatus (red-bellied tamarin)
		S. imperator (emperor tamarin)
		S. midas (golden-handed tamarin)
		S. fuscicollis (saddle-backed tamarin)
		S. nigricollis (black-mantled tamarin)
		S. triparitus (golden-mantled saddle-backed tamarin)
		S. inustus (mottle-faced tamarin)
		S. bicolor (pied/bare-faced tamarin)
		S. oedipus (cotton-top tamarin)
		S. leucopus (white-footed tamarin)
		S. geoffroyi (Geoffroy's tamarin)
	Leontopithecus	*L. rosalia* (golden lion tamarin)
		L. chrysomelas (golden-headed lion tamarin)
		L. chrysopygus (black lion tamarin)
		L. caissara (black-faced lion tamarin)
	Callimico	*C. goeldii* (Goeldi's monkey)

With regard to species and subspecies, taxonomic designation is still disputed [3]. However, it is generally agreed that the genus *Saguinus* is one of the largest and most diverse platyrrhine lineages (e.g., Hershkovitz, 1977, 1979, 1982; Mittermeier *et al.*, 1988). In this thesis, the genus *Saguinus* contains 32 taxonomic forms of 12 species as listed in Rylands (1995) (see Table 1.3).

A major controversy in the evolution of the Platyrrhini has centred on the question of the derived or primitive nature of the callitrichine radiation (Garber, 1993a). It has been suggested that callitrichines represent the most primitive of extant primates, relatively little diverged from ancient anthropoid stock (e.g., Hershkovitz, 1977). At present, however, there is a growing consensus that the combination of traits, common to most species within this subfamily (see Table 1.4), instead represent a set of derived and highly specialised adaptations evolved in response to a particular ecological niche, that is, marginal and disturbed forest habitats (Garber 1980, 1984a, 1993a; Sussman & Kinzey, 1984; Rylands *et al.*, 1993; Rylands 1996). For example, all tamarins possess pointed, keeled, claw-like tegulae (nails) on all manual and pedal digits, excepting the hallux (big toe) (Ford, 1980), and use them to support themselves when on large vertically or sharply inclined substrates (Pook & Pook, 1982; Snowdon & Soini, 1988; Thorington, 1988). This trait enables them to utilise a series of resources, such as certain insects and plant exudates, which are typically harvested from the wide trunks and boughs of large trees in the lower forest stratum (Garber, 1980). Aside from distinguishing morphological characteristics such as

---

[3] Disagreement exists as to whether *S. geoffroyi* is correctly classified as a discrete species (Mittermeier *et al.*, 1988; Eisenberg, 1989; Rylands *et al.*, 1993) or as a subspecies of *S. oedipus* (Hershkovitz, 1977), and whether *S. tripartitus* is correctly classified as a discrete species (Mittermeier *et al.*, 1988; Thorington, 1988; Rylands *et al.*, 1993) or a subspecies of *S. fuscicollis* (Hershkovitz, 1977).

Table 1.3: Number of subspecies of the twelve species of the genus *Saguinus* as listed in Rylands (1995).

Scientific Name	**Common Name**	**Number of Subspecies**
Saguinus mystax	moustached tamarin	3
Saguinus labiatus	red-bellied tamarin	2
Saguinus imperator	emperor tamarin	2
Saguinus midas	golden-handed tamarin	2
Saguinus fuscicollis	saddle-backed tamarin	12
Saguinus nigricollis	black-mantled tamarin	3
Saguinus triparitus	golden-mantled saddle-backed tamarin	1
Saguinus inustus	mottle-faced tamarin	1
Saguinus bicolor	pied/bare-faced tamarin	3
Saguinus oedipus	cotton-top tamarin	1
Saguinus leucopus	white-footed tamarin	1
Saguinus geoffroyi	Geoffroy's tamarin	1

Table 1.4: Biological and behavioural traits characteristic of the primate subfamily Callitrichinae (adapted from Garber, 1993).

Small body size
Claw-like nails (tegulae) on all manual and pedal digits, excluding the hallux, which bears a flattened nail
Ability to adopt a clinging posture on large vertical supports
Loss of third maxillary and mandibular molars
Upper molars tritubercular and lacking a hypocone
Procumbent lower incisors with thick labial enamel and an absence of enamel on the lingual aspect [1]
Reproductive twinning [2]
High ratio of foetal weight to maternal body weight [2]
Ability to produce young twice during the year
Evidence of suppressed ovulation among subordinate adult female troop members [3]
Extensive male assistance in infant care
Helpers and communal care of the young

[1] Found only in the marmoset genera *Cebuella* and *Callithrix.*

[2] Present in all genera except *Callimico.*

[3] Although not for *Leontopithecus rosalia* (French, 1987; Baker, 1991).

these, many features of tamarin locomotor, postural and other behaviour, and their ecological and social organisation, may also be relatively recent and interrelated adaptations rather than the retentions of primitive New World primate ancestors (Moynihan, 1976; Szalay & Delson, 1979).

The evolutionary history of the Callitrichinae is thought by some to be characterised by a process of phyletic dwarfism and it has been suggested that many of the aforementioned callitrichine character traits are a direct result of this phyletic dwarfism and the constraints that reduced body size produces on diet, foraging strategies and reproductive success (Leutenegger, 1973, 1979, 1980; Eisenberg, 1978; Rosenberger, 1977, 1981; Ford, 1980, 1986). For example, Leutenegger (1979) believes that the ancestors of the Callitrichinae were larger in body size than any of the extant species, were frugivorous, and that a shift to an insectivorous diet caused selection for a smaller body size. Dependence upon fruit and insect prey, and variations in the availability of these resources due to, for example, seasonality, distribution and habitat location, in turn determined callitrichine ranging and foraging patterns. Similarly, Menzel and Juno (1985) propose that severely limited space and food resources, and competition for these resources, are the most obvious candidates for the ultimate selective forces that might have led to dwarfing. However, Garber (1993a) points out that, although dwarfing is likely to have been an important factor in callitrichine evolution, it provides only partial explanation for the existence of the callitrichine traits (because they appear to be adaptations to a particular ecological niche and they do not necessarily parallel those found in other lineages of small (not necessarily dwarfed) primates). Sussman and Kinzey (1984) go as far as to claim that callitrichines are not necessarily phyletic dwarfs at all. They argue that, instead, each of the callitrichine traits can be explained by forms of selection other than selection for small size. In favour of this view, callitrichines do not have the relatively large brains which are expected in phyletic dwarfs (Clutton-Brock & Harvey, 1980).

1.2.2 Geographical Distribution and Association Patterns

At the present time, callitrichine distributions are poorly understood and based, in many cases, on very few locality records (Rylands *et al*., 1993). In general, tamarins are found throughout the tropical and sub-tropical forests of Central and South America, their geographical distribution straddling the equator, from as far north as 9° N (Panama, Costa Rica), to as far south as 24° S (Bolivia, Brazil) (Hershkovitz, 1977) (see Figure 1.1). However, this distribution is not continuous and appears to be limited by major rivers (Ayres & Clutton-Brock, 1992; Peres *et al*., 1996). More specifically, tamarins exploit a wide range of primary, secondary and edge habitats from Western Panama throughout much of the Amazon Basin of Colombia, Ecuador, Peru, Bolivia, and Brazil (Hershkovitz, 1977; Mittermeier & Coimbra-Filho, 1981; Snowdon & Soini, 1988). In fact, a mix of forest types appears to be an essential requirement of tamarin ecology and a preference for areas with a high ratio of edge to non-edge vegetation has been noted for many species (e.g., *S. fuscicollis*, *S. labiatus*, *S. mystax*, *S. geoffroyi* (Geoffroy's tamarin): Izawa & Bejarano, 1981; Izawa & Yoneda, 1981; Mittermeier & Roosmalen, 1981; Terborgh, 1983; Snowdon & Soini, 1988). With regards to this, Rylands (1987, 1996) argues that tamarins may have evolved to occupy secondary growth forest patches (gaps arising from tree falls) and other edge habitats, and that a need for microhabitat diversity probably reflects differences in the temporal and spatial distribution of their food types (mainly insects and ripe fruits) as well as the particular manner in which they exploit their environment.

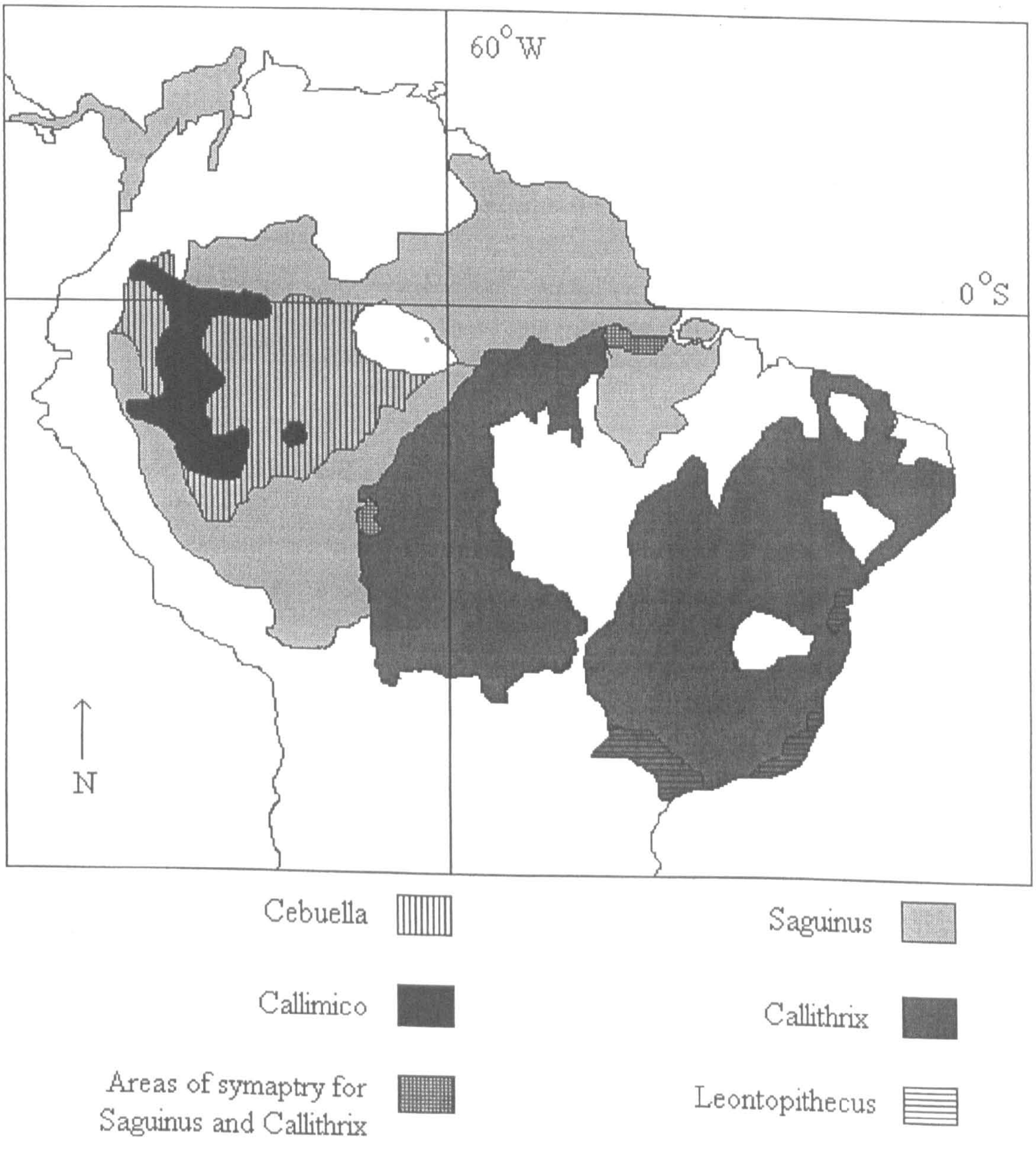


Figure 1.1: Sketch map showing the geographical distribution of the callitrichine genera, including *Saguinus* (adapted from Hershkovitz, 1977, and Kinzey, 1997).

Thick secondary growth provides exuberant successions of food plants and animal prey, and typically contains high densities of colonising fruiting species which supply small animal-dispersed fruits over long fruiting seasons (Opler *et al.*, 1980). Small quantities of fruits, available for extended periods of time within a restricted area, are perfect for tamarins but not for larger primates. In addition, the dense vegetation of secondary growth and edge habitat provides tamarins with cover and torturous escape-ways that are impenetrable or intransitable to most of their large predators (Hershkovitz, 1977). It also represents the best structural environment for tamarins to move around their home ranges (Rylands, 1996).

S. fuscicollis, the most diminutive of the tamarins (250 - 400 g: Snowdon & Soini, 1988), has the widest distribution of all tamarin species (Hershkovitz, 1977), and is found east of the Cordillera Oriental in Colombia, Ecuador, Peru, Bolivia, western Brazil, and both north and south of the Río Amazonias (Ferrari & Lopes-Ferrari, 1992; Rylands *et al.*, 1993). This range encapsulates entirely the distribution of the three members of the *S. mystax* group (*S. mystax*, *S. labiatus*, *S. imperator*: Hershkovitz, 1977) (see Figure 1.2) who are larger than *S. fuscicollis* (450 - 650 g: Snowdon & Soini, 1988; Garber, 1993a). These three species are mostly allopatric with each other, and thus do not form mixed-species troops with each other, but almost always form mixed-species troops with *S. fuscicollis* at all sites where they co-occur (Peres, 1991) (see Table 1.1). Hershkovitz (1977) suggests that opportunities for association arose within the genus *Saguinus* following high rates of speciation, resulting in the co-occurrence of congeners throughout their geographical ranges.

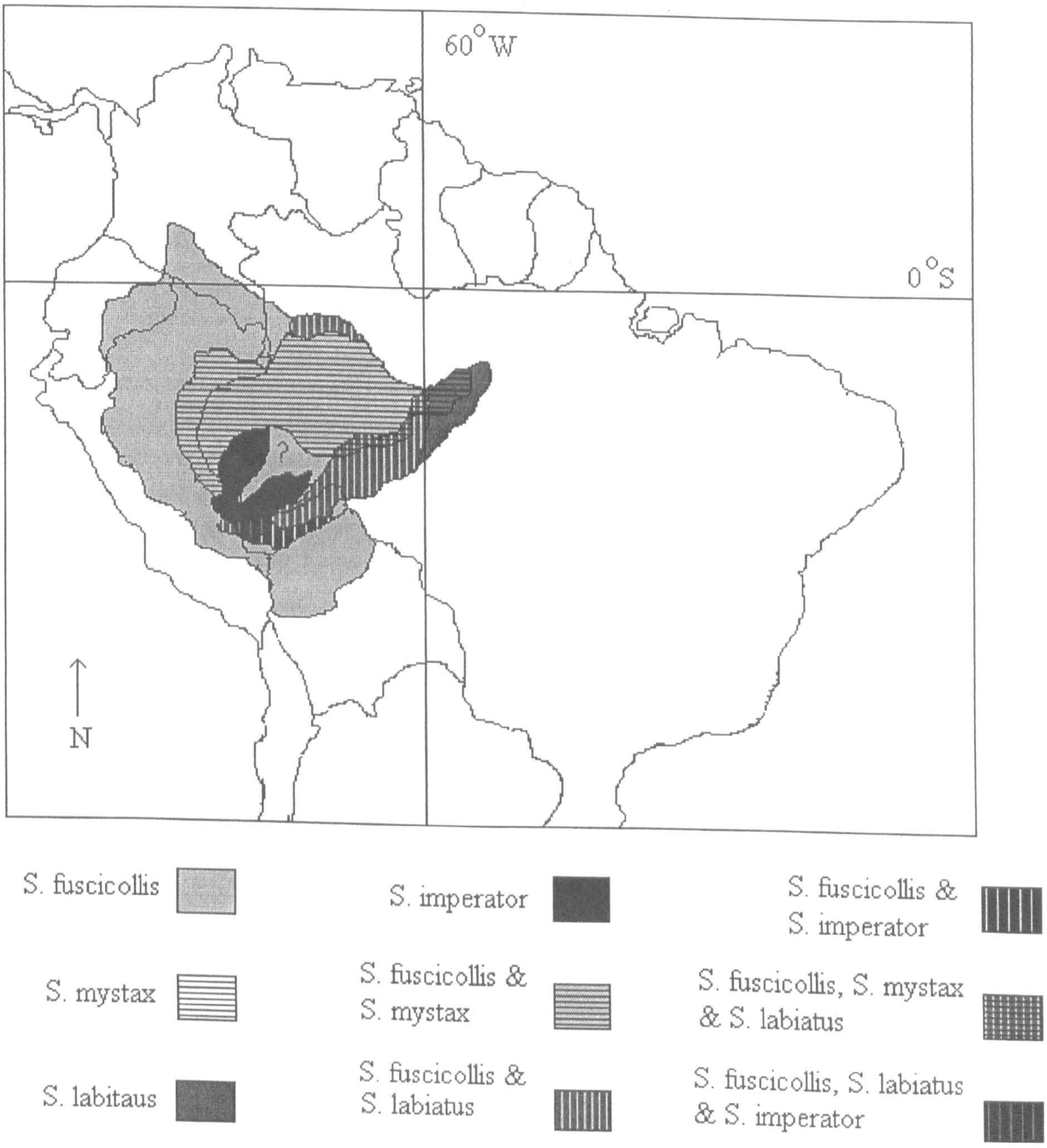


Figure 1.2: Sketch map showing the geographical distribution of *S. fuscicollis* and the three members of the *S. mystax* group (*S. mystax*, *S. labiatus*, *S. imperator*) (adapted from Hershkovitz, 1977).

Competition theory predicts that, under resource-limited conditions, associated heterospecifics (which potentially encounter equal units of the same resources at equal rates) should segregate ecologically to a certain degree, or else their long-term coexistence could be threatened by competitive exclusion (e.g., Gause, 1934; May, 1973). In this regard, it has been suggested that the ecological similarity of the three species in the *S. mystax* group argues against sympatry between them, especially given their sympatry with *S. fuscicollis* (Rylands, 1987). There may not be sufficient niche differentiation between these closely related species to ameliorate the increased feeding competition that would result from associating. However, patterns of resource use by associated heterospecifics cannot be too divergent because the costs of forming and maintaining their association would become prohibitive. Overlap in resource use thus also provides room for potentially intricate inter-specific interactions. The level of stability of an association, given its initial chances of occurring at all, may then reflect a balanced trade-off between advantageous interactions and disadvantageous interactions arising from similarities between the participating species (Hardie, 1995). Inter-specific similarities in behaviour and ecology do seem to contribute positively to the permanence and stability of the mixed-species troops formed between *S. fuscicollis* and the members of the *S. mystax* group (Norconk, 1990b). For example, associating tamarin species usually move about the troop's home range as a single cohesive unit (typically within 20 - 50 m of each other: Buchanan-Smith, 1990a; Heymann, 1990a) and both species use vocal communication to maintain intra-troop cohesion (Castro & Soini, 1978; Pook & Pook, 1982; Norconk, 1986); both species respond to each other's alarm calls (Terborgh, 1983; Heymann, 1987; Buchanan-Smith, 1990a; Peres, 1993a; Windfelder, 1997); there is high overlap in the percentage of plant species used (Terborgh, 1983; Garber, 1988b; Ramirez, 1989; Hardie, 1998); and both species are aggressive to conspecifics in neighbouring troops (Norconk, 1986), defending their shared home range in parallel against these troops (Terborgh, 1983; Yoneda, 1984a; Garber, 1988b; Buchanan-Smith, 1990a; Peres, 1992a).

S. fuscicollis can also occur sympatrically with *S. nigricollis* (black-mantled tamarin) (Hershkovitz, 1977; Izawa, 1978), and mixed-species troops have been reported to occur between these species (Hernández-Camacho & Cooper, 1976). However, this association has yet to be confirmed by other studies, and moreover, the authors do not define explicitly what is meant by 'mixed-species association' in spatio-temporal terms, or what it is that the species do when together. Heymann (1997) argues that it is highly unlikely that these two species form stable mixed-species troops like those formed between *S. fuscicollis* and the members of the *S. mystax* group because they are morpho-ecologically too similar, particularly with regard to foraging for insect prey.

S. fuscicollis may also form associations with heterogeneric species. However, these appear not to be as stable or long-lasting as those with congeneric species, probably due to (overly) divergent ecological niches. For example, the geographical range of *S. fuscicollis* overlaps with that of *Callimico* and reports have been made of tri-specific associations between these two species with *S. mystax* in Peru (Encarnación, pers. comm. to Heymann) and *S. labiatus* in north-west Bolivia and south-east Peru (Pook & Pook, 1982; Cameron *et al.*, 1989; Buchanan-Smith, 1991a; Garcia & Cases, 1989; Christen & Geissmann, 1994). However, whilst associating tamarin species usually form mixed-species troops with only one congeneric troop, that is, the same pair of troops associate consistently, patterns of association for *C. goeldii* are different. For example, in situations where the larger home range of *C. goeldii* encompasses the home ranges of a number of tamarin mixed-species troops, it may form loose associations with more than one them (Pook & Pook, 1982; Garcia & Cases, 1989).

Marmosets and tamarins are mostly allopatric with each other, each genus being distributed on different sides of the Río Madeira border (Hershkovitz, 1977; but see de Vivo, 1985). As a result, little opportunity for association between them exists. *S. midas* (golden-handed tamarin) is sympatric with *Callithrix argentata* (silvery/bare-ear marmoset) in the flood-plain of the Tocantins-Xingu interfluvium, Brazil, but there are no reports of mixed-species associations for these species (Ferrari & Lopes-Ferrari, 1990b). However, *S. fuscicollis* and *Callithrix emiliae* (Snethalge's marmoset) are found sympatrically and have been reported to associate in the state of Rondônia, Brazil (Martins *et al.*, 1987; Lopes & Ferrari, 1994). On the question of this association, 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, as is the case with *S. fuscicollis* and *S. nigricollis* mixed-troops, the actual details of the association are unclear. Marmosets share many characteristics with tamarins, such as the production of twin infants (Rylands, 1981, 1984) and an omnivorous diet (Hubrecht, 1984) but, unlike tamarins, they possess dentition specialised for gouging holes in trees to stimulate exudate flow (Coimbra-Filho & Mittermeier, 1976, 1978; Sussman & Kinzey, 1984; Stevenson & Rylands, 1988). With dental specialisations absent, tamarins, when feeding on exudates, must do so opportunistically. Ferrari and Lopes-Ferrari (1989) have proposed that this fundamental difference between marmosets and tamarins has far-reaching implications for many aspects of their ecology, behaviour and ultimately, social organisation. As a result, marmosets and tamarins may be unable to form permanent and stable mixed-species troops.

Leontopithecus chrysomelas (golden-headed lion tamarin) is sympatric with *Callithrix* *kuhli* (Wied's black-tufted-ear marmoset) and may form mixed-species troops, although these are considered to be much more ephemeral than those between *S. fuscicollis* and the members of the *S. mystax* group (Rylands, 1989).

The tiny *Cebuella* does not form mixed-species troops with tamarins despite sympatry with five tamarin species (Ferrari, 1993). This is possibly due to large differences in body size, diet and home range size (Izawa, 1975; Ferrari & Lopes-Ferrari, 1989; Soini, 1993). Thus, we have a pattern emerging regards association between sympatric callitrichines. Only those associations between *S. fuscicollis* and the members of the *S. mystax* group appear to be consistent, stable and long-term.

1.2.3 Mating Systems and Social Organisation

Until very recently, monogamy was assumed to be the keystone of tamarin (indeed, all callitrichine) social organisation. Like most callitrichines, tamarins exhibit little sexual dimorphism (Hershkovitz, 1977) and reproduce in captivity most successfully when housed in monogamous pairs with their offspring. Historically, these findings gave rise to the widespread assumption that wild tamarins typically live in stable monogamous pairs (e.g., Kleiman, 1977; Dawson, 1978; Neyman, 1978) and are exclusively (or mostly) monogamous (e.g., Epple, 1978a; Neyman, 1978). Although debate currently exists concerning tamarin mating systems (see Price, 1990a, for a detailed discussion), recent evidence now favours a more complex and variable form of social organisation than simple monogamy. It appears that tamarins can be monogamous, polygynous, or polyandrous, depending on some combination of social and ecological factors that are not yet well understood (Goldizen, 1987a,b, 1988, 1989; Garber *et al.*, 1991, 1993b; Ruth, 1991).

Despite this flexibility in mating system, in general, tamarin troops have only a single female breeding at any one time (e.g., Yoneda, 1981, 1984a,b; Pook & Pook, 1982; Widowski *et al.*, 1990). This is true of all species for which there are relevant data (although there are occasional, and important, exceptions to this general rule: see Terborgh & Goldizen, 1985, for *S. fuscicollis*; Ramirez, 1984; Garber *et al.*, 1991, for *S. mystax*). It is believed that all other females in the troop are reproductively suppressed by the breeding female, probably through an olfactory mechanism as occurs in some captive troops. For example, scent marks have been confirmed as one of the means by which dominant breeding females inhibit reproductive activity in subordinates in captive *S. fuscicollis* (Epple & Katz, 1984) and *S. oedipus* (cotton-top tamarin) (French *et al.*, 1984), but mechanisms may vary between genera and species (Abbot *et al.*, 1993). There is no known comparable endocrine suppression for male tamarins (Sussman & Garber, 1987).

Tamarins are predominantly seasonal breeders and typically give birth to non-identical twin infants early in the rainy season (around the time of maximum fruit abundance) (Hershkovitz, 1977; Pook & Pook, 1981; Terborgh, 1983; Soini, 1987b). Births do occur at other times, but relatively few births occur in the resource-limited dry season (Moynihan, 1970; Peres, 1991). Tamarin neotonates are relatively large when compared to the mother's bodyweight (14 to 25 % of the mother's weight: Leutenegger, 1973; Kleiman, 1977) and are, as such, extremely energetically costly to produce. The costs of reproduction is further inflated for female tamarins because they usually have a postpartum oestrus (Hershkovitz, 1977). This often equates to lactating females becoming gravid, and thus investing in two sets of twins at once. Furthermore, dietary resources for tamarins (mainly fruits and insects) are widely dispersed both spatially and temporally, and this means that infants may have to be carried if they are to remain with the group over a necessarily long daily foraging path (Epple, 1975b; Tardif, 1994; Pryce, 1988; Price, 1990b). High infant weight and a possible postpartum oestrus, coupled with increased foraging demands resulting from lactation and the need for intensive carrying of usually two infants during their first 10 - 12 weeks, may mean that lone females, and perhaps single pairs, are unable to rear offspring on their own (Goldizen, 1987a,b; Snowdon & Soini, 1988). It has been proposed that, as a consequence, tamarins are communal rearers, with much of the infant care being provided by the breeding male and non-parent helpers (often older offspring), and that this need for helpers in infant care shapes the mating system and social structure in tamarins (e.g., Goldizen & Terborgh, 1989; Tardif *et al.*, 1993). For example, Goldizen and Terborgh (1989) have argued that *S. fuscicollis* pairs are unable to raise twins successfully without helpers, thus a polyandrous mating system is the only and logical consequence. They propose that troops without non-reproductive helpers, such as newly formed pairs, may typically accept another male as a second breeder and helper. By sharing the probability of fathering young (di-zygotic twinning), and then helping to care for them, co-operating males may enhance their mutual reproductive success (the original male increasing reproductive success in the short term, that is, until offspring helpers are present).

The proposition that tamarin parents accrue reproductive benefits from helpers is largely undisputed, despite assessment of the real qualitative and quantitative relief provided to the breeding pair or female from helpers being very difficult. With respect to additional care-givers increasing breeding success, however, Garber *et al.* (1984) demonstrated a positive correlation between the number of adult helpers and infant survival in wild *S. mystax* troops. (A similar positive correlation has been observed between the number of adult males per troop and reproductive success of the troop (number of juveniles) for *Callithrix jacchus* (common marmoset): Koenig, 1995). The helpers carry infants, share food with them, and may also play with, clean, groom, and defend them against predators (Feistner, 1985; Goldizen & Terborgh, 1985; Goldizen, 1987a; Savage *et al.*, 1989; Feistner & Price, 1990; Heymann, 1990c; Price, 1990a; Peres, 1991). In so doing, the metabolic cost of infant ontogeny is effectively distributed among the troop members, and some of the breeding female's reproductive effort can be re-directed quickly to the next litter (Garber & Leigh, 1997). The question: is a specific mating/breeding system required to guarantee optimal infant care?, is a more contentious issue. For example, Rothe and Darms (1993) point out that subsequent field data do not substantiate the assumption of Goldizen and Terborgh (1989) that lone *S. fuscicollis* pairs are unable to raise infants, and that paternal care determines the mating/breeding system. Rather, all that Goldizen and Terborgh demonstrate, according to Rothe and Darms, is that pair/trio formation in *S. fuscicollis* is a rare event (for whatever reason). Moreover, they suggest that Goldizen and Terborgh admit indirectly that *S. fuscicollis* pairs may be able to rear offspring on their own when they write

> *"even if the parents were capable of doing all of the infant-carrying, the helper's aid might allow the parents to conserve energy, survive longer and/or breed again sooner than would otherwise be possible"* (p. 297)

Whatever the eventual outcome of the debate, as noted by Rylands (1996), the key to understanding the evolution of both social and reproductive behaviour in tamarins probably lies in an understanding of their habitats and the resources bases within them.

But why should helpers help? In addition to costs incurred from the time invested in offspring, there is a significant metabolic expense from carrying infants of such high weight (Kirkwood & Underwood, 1984; Goldizen, 1987a); reduced mobility, especially when carrying twins, that may interfere with travel (Price, 1992); and an additional foraging cost as tamarins usually eat less when carrying infants (Goldizen & Terborgh, 1986). The most frequently proposed explanations for the occurrence of helping in callitrichines, despite these costs, are the following:

(a) A gain in rearing experience (Cleveland & Snowdon, 1984; Epple, 1975a,b, 1978a,b; Tardif *et al.*, 1984; Goldizen, 1988; Baker, 1991; Abbot *et al.*, 1993). Helping parents or unrelated individuals to care for their infants may provide one with the necessary rearing experience to raise one's own offspring successfully.

(b) A contribution to inclusive fitness via kin selection (Hamilton, 1964; West Eberhard, 1975; Terborgh & Goldizen, 1985; Goldizen, 1988; Baker, 1991). Breeding vacancies in tamarin populations are limited (Abbot *et al.*, 1993), and it has been suggested that dispersal is risky due to high predation rates (Sussman & Kinzey, 1984; Goldizen & Terborgh, 1989). Under these conditions, the best strategy for siblings and other related individuals may be to increase their inclusive fitness by remaining in the natal troop and assisting their relatives to raise offspring. In opposition to this suggestion, Sussman and Garber (1987), referring mainly to the studies of Terborgh and Goldizen (1985) with *S. fuscicollis* and Garber *et al.* (1984) with *S. mystax*, argue that migrations are regular events in tamarin societies. Yet, in a later study on *S. mystax*, Ramirez (1989) failed to find high rates of migration. Rothe and Darms (1993) argue that sufficient data on migration rates and the identity of dispersing individuals are not yet available to make any sound conclusions. However, they do say that, while accepting a certain fluctuation in membership, results of the majority of field studies indicate the births and deaths, rather than dispersal events, are the decisive variables concerning the structure of tamarin families/troops.

(c) Delayed benefits through reciprocal altruism (Trivers, 1971; Axelrod & Hamilton, 1981; Baker, 1991). Rylands (1982), Price (1990a) and Ferrari (1992) consider the provision of infant care in callitrichines as a form of submissive behaviour towards the breeding female to ensure permanence in the troop. In this regard, Box *et al.* (1995) and Box (1997) have observed male *C. jacchus*, *S. fuscicollis*, *S. labiatus* and *S. oedipus* deferring to females during feeding. They suggest that, whilst the breeding male may defer to the breeding female to aid the survival of their investment (offspring), non-breeding males may defer to the breeding female or potentially breeding females in order to 'stay around' in terms of mating opportunities (a promise of future dominance status). Social deference to the breeding female makes sense in the context of a communal rearing system that supports the heavy energetic demands of pregnancy, multiple births and lactation (Sussman & Garber, 1985) and is advantageous when there is a small number of potentially successful male partners (Box *et al.*, 1995).

(d) An option to 'inherit' breeding status in the native troop, or part of the home range by annexing (Emlen & Vehrencamp, 1985; McGrew & McLuckie, 1986; Sussman & Garber, 1987; Baker, 1991). The bequeathing of part of the home range may provide a helper with an opportunity to form a new troop in which he/she can establish himself/herself as a breeding individual. Alternatively, helpers may attain a breeding position in their native troop following the death of one or more breeding individuals. Rothe and Darms (1993) consider this explanation unlikely given the rare occurrence of inheritance, the rather long tenure of the breeding pair (Rylands, 1982, 1986a; Soini, 1982, 1987b, 1988; Hubrecht, 1984, 1985; Ferrari, 1988; Stevenson & Rylands, 1988), and the fact that only one position in either sex class may be replaced. They suggest that these factors argue against inheritance as an adaptive strategy, quite apart from the deleterious effects of inbreeding.

1.2.4 Foraging Behaviour

In this section I shall discuss the foraging strategies of tamarins in general and then go on to examine the main components of their diet in detail.

Tamarins are *foragers*, that is, their feeding behaviour requires that they devote a large portion of their time to searching for (and for animal prey, capturing) their food. Much of the diet of primate foragers comes from small, highly dispersed food patches. The omnivorous diet of tamarins is no exception, consisting of a wide variety of dispersed foods, including insects, small vertebrates, ripe fruit, plant exudates (e.g., gums and sap) and nectar (Kinzey, 1986; Snowdon & Soini, 1988; Garber, 1993a). Although predominantly frugivore-insectivores (Terborgh, 1983; Peres, 1993b), during times of fruit scarcity tamarins may switch to nectarivory (Terborgh & Stern, 1987; Peres, 1994) or gummivory (Garber, 1993a,b), relying on certain keystone resources such as the flowers of *Symphonia globulifera* (ossol) (for nectar) and the pods of *Parkia* species (for gum) to sustain them until fruit is again abundant (Garber, 1988a,b, 1993b; Buchanan-Smith, 1990a; Heymann, 1990a; Peres, 1991).

The foraging strategies of tamarin species are quite different from those of other primate taxa, and in some cases from one another (Dawson, 1979; Izawa, 1978; Mittermeier & Roosmalen, 1981; Terborgh, 1983). When insect foraging, tamarins typically prey on large (25 - >50 mm) mobile insects, in particular orthopterans (grasshoppers, locusts, crickets and katydids), in the dense vegetation of the lower forest strata (e.g., Terborgh, 1983; Crandlemire-Sacco, 1986; Peres, 1993b). In this environment they are able, by virtue of their small size, to hunt for these insects by stealth more efficiently than the larger insectivorous platyrrhines such as *Cebus* (capuchins) and *Saimiri* (squirrel monkeys) (Terborgh, 1983). Capturing relatively large prey enables them to maintain a large proportion of animal material in their diet while spending less time foraging, and thus effectively follow a time-minimising foraging strategy (Schoener, 1971) appropriate for small animals which are thought to be highly vulnerable to predation (Terborgh, 1983; Cheney & Wrangham, 1987; Peres, 1993a).

All plant material is exploited selectively, that is, when feeding on reproductive plant parts or exudates, tamarins typically concentrate on a relatively small number of the total plant species available to them at any one time (Rylands, 1982; Terborgh, 1983; Soini, 1987). For example, Terborgh (1983) who studied *S. fuscicollis* and *S. imperator* in the forests around Cosha Cashu, a remote Peruvian lake, found that both species tended to feed on fruit from one to three plant species at a time, regardless of how many alternative resources where available within their territories. In fact, with regards to fruit resources, tamarins again appear to have a unique strategy, compared to other platyrrhines, in that many of the most frequently exploited fruit resources are small trees or lianas which produce relatively small fruits in tiny, scattered, incremental units (Garber, 1993a). Furthermore, these resources ripen in a 'piecemeal' fashion (Opler *et al.*, 1980), that is, in small quantities over relatively long periods. The distribution of these resources, in space and time, renders them unattractive for systematic exploitation by larger-bodied platyrrhines, thereby reducing potential competition. Piecemeal ripening implies that only a very small amount of food is available for eating at any given locus on any single occasion, and also that a reliable, though scant, supply can be obtained at the same loci over a period of many weeks. This, together with small body size, enables tamarins to trapline their fruit (and nectar) resources (a behaviour whereby decisions regarding the use of particular feeding trees are based principally upon minimising the distances travelled between them). Since fruit is the principle plant resource consumed by tamarins, Terborgh (1983) believes such factors are of the utmost significance for understanding the behavioural, social and ecological organisation of tamarins more generally. He writes (but see also Milton, 1981; Richard, 1981)

> *"the most important characteristic of fruit from the point of view of differential exploitation by primates is not its size, texture, colour, construction or taxonomic status,* [but] *its characteristic degree of concentration in space and time"* (p. 95).

Tamarins are highly skilled in their knowledge of the position of food trees, and make use of a complex spatial memory and/or cognitive maps to forage efficiently in a highly complex environment (Dolins, 1993; Garber, 1988a, 1989; Garber & Hannon, 1992; Garber *et al.*, 1993b; Garber & Dolins, 1996). Garber (1989) argues that by maintaining a detailed knowledge of the distribution and location of many tree species in their home range, *S. fuscicollis* and *S. mystax* can offset the patchiness of the fruit (and exudate) part of their diet through goal-directed foraging and an ability to compare accurately the distances from their present location to a large number of potential feeding trees.

(a) Animal Prey

As predators, tamarins are bold and aggressive and animal prey is an essential and critical component of the tamarin diet. Due to their small size, quick, jerky movements and sharp, 'claw-like' tegulae, they are eminently suited for the efficient capture of insects, and their tritubercular molars are efficient tools for cracking chitinous exoskeletons. Aside from insects, tamarins have also been known to capture small lizards, frogs and birds, and to consume eggs opportunistically (Neymann, 1978; Pook & Pook, 1982; Snowdon & Soini, 1988; Peres, 1992b). As food, animals provide a plentiful supply of high-quality protein, lipids and fluid. It is for this reason that animal prey represents the highest-quality dietary component of wild tamarins, even though plant material makes up most of their diet (Yoneda, 1981; Terborgh, 1983; Peres, 1992b; Rylands, 1990).

Insects are the animal prey most commonly eaten by tamarins, accounting for 30 - 77 % of total feeding and foraging time (Garber, 1980, 1984a, 1988a,b; Mittermeier & Roosmalen, 1981; Soini & Coppula, 1981; Terborgh, 1983; Soini, 1987; Snowdon & Soini, 1988), many species of which provide a dependable source of proteins and lipids throughout the year. In addition, insects with exoskeletons are also a rich source of carbohydrates for species able to digest chitin. From a primate's perspective, insects are small and often highly mobile, and their harvest demands considerable skill. They tend to exhibit a patterned or scattered distribution, and marked temporal population cycles (Price, 1975; Leigh & Smythe, 1978). However, the insect foraging patterns of tamarins show that, although insects may be scattered widely, they do not occur randomly (for example, *S. fuscicollis* focus their insect foraging activities on nooks and crannies of tree trunks: Terborgh, 1983). Troop members forage for insects independently (Garber, 1980; Yoneda, 1984b; Soini, 1987) and foraging success appears to be dependent upon selecting appropriate areas of the forest and times of the day when the opportunity for prey detection and capture are high, rather than any co-ordinated co-operative action (Garber, 1993a).

Comparisons of species-specific differences within the genus *Saguinus* have provided evidence for at least three distinct insect foraging patterns (Garber, 1993a):

(1) *S. fuscicollis*, and possibly *S. nigricollis* and *S. bicolor* (pied/bare-faced tamarin), exhibit the most distinctive pattern exploring trunks and other large, vertical substrates in search of relatively large (25 - >50 mm), cryptic (bark-mimicking) and hidden (wood boring or refuging) prey (Izawa, 1978; Terborgh, 1983; Yoneda, 1984b; Crandlemire-Sacco, 1986; Soini, 1987; Snowdon & Soini, 1988). By virtue of their relatively small size, together with their elongated and laterally compressed 'claw-like' tegulae, *S. fuscicollis* is able to use a combination of vertical clinging postures and scansorial locomotion to manually explore closed and concealing microhabitats such as knotholes, crevices and other such regions of the trunk. Vertical surfaces also serve as a perch from which to locate terrestrial prey. Insects are procured in all levels of the forest, although 25 - 75 % of insect foraging is reported to occur at a height of less than 6 metres above the ground (Terborgh, 1983; Yoneda, 1984a, 1984b; Norconk, 1986; Soini, 1987; Garber, 1998b).

(2) Species of the *S. mystax* group (*S. mystax*, *S. labiatus*, *S. imperator*), and possibly *S. midas*, exploit open and exposed microhabitats (leaves and branches in the lower and middle levels of the forest canopy) for mobile insects (Mittermeier & Roosmalen, 1981; Yoneda, 1981, 1984a; Terborgh, 1983; Garber, 1988b). They utilise a visual searching technique together with rapid foraging movements, such as lunges and pounces. In contrast to pattern (1), Garber (1993a) reports that, for *S. mystax*, less than 1 % of insect prey are captured below 6 metres (49 % are captured above 15 metres in height). Divergent insect foraging behaviour is likely to be the key, or at least an important factor,

permitting sympatry between *S. fuscicollis* and the members of the *S. mystax* group (Heymann, 1997) and will be discussed in more detail in later chapters.

(3) The third pattern is exhibited by *S. geoffroyi*. Insects are hunted on thin flexible branches in the low shrub layer of the forest understory, some 1 - 5 metres above the ground, using a series of energetically costly locomotor and postural activities. Prey are captured by moving cryptically, with minimal disturbance, in the understory and then strikingly rapidly with the forelimbs while the hindlimbs maintain a firm grasp on the supporting vegetation.

(b) Fruit Resources

Ripe fruits are a high-energy resource, rich in non-structural carbohydrates and simple sugars, and account for 20 - 65 % of total feeding time in all tamarin species studied (Garber, 1993a). Fruits of the genus *Cecropia* and *Pourouma* represent important food resources in many tamarin species, but are rare in the diet of other New World monkeys (Garber, 1993a). The majority of tamarin fruit (and nectar) feeding takes place on small to moderate-sized branches in the periphery of the tree crown (*S. fuscicollis*: Crandlemire-Sacco, 1986; Garber, 1986, 1987, 1988a,b; *S. labiatus*: Yoneda, 1981, 1984a; *S. mystax*: Garber, 1986, 1988a,b; *S. imperator*: Terborgh, 1983). In contrast to insect foraging, *S. fuscicollis* and the members of the *S. mystax* group all forage for fruit at around the same height, avoiding the lower layers of the forest (Garber, 1993a).

Many of the fruit species eaten by tamarins are drupes or arillate fruits which contain a single, or small number of, large seeds (Terborgh, 1983; Crandlemire-Sacco, 1986; Garber, 1986; Soini, 1987; Snowdon & Soini, 1988). The frequency with which the seeds are ingested appears to vary between species but, like many species of primates, tamarins do appear to play an important role in seed dispersal; voided seeds exhibiting high germination success (Hladik & Hladik, 1969; Crandlemire-Sacco, 1986). Knogge *et al.* (1998) found mixed-species troops of *S. fuscicollis* and *S. mystax* in north-eastern Peru to disperse the seeds of at least 92 identified plant species from 35 families.

When feeding on fruits, tamarins exhibit two distinct patterns of resource exploitation (Pook & Pook, 1982; Soini, 1987; Garber, 1988b, 1989):

(1) Very small-crowned feeding trees are fed in opportunistically, by one or a few troop members, and are rarely re-visited. For example, in mixed-species troops of *S. fuscicollis* and *S. mystax*, 55 % of all trees/lianas fed in during a three-month period were visited on only one occasion (Garber, 1988b). Single-species troops of *S. fuscicollis* have been found to exhibit a similar pattern (Crandlemire-Sacco, 1986; Soini, 1987). Such resources are rarely defended from other troops and their overall contribution to the diet is small.

(2) The second group of fruit species appear to be the primary focus of feeding and ranging activities. *S. fuscicollis, S. labiatus, S. mystax, S. imperator*, and *S. geoffroyi* concentrate their daily feeding efforts on many scattered individual trees from a small number of tree species. These resources are exploited in a co-ordinated manner with trees of the same species often being visited during successive feeding bouts. Whilst feeding, aggression is minimal, with all or most troop members feeding in the same tree at the same time (Janson *et al.*, 1981; Terborgh, 1983, 1985; Yoneda, 1984b; Crandlemire-Sacco, 1986; Garber, 1986, 1988a,b; Soini, 1987).

(c) Exudate and Nectar Feeding

Many species of callitrichines consume plant exudates. Sap is procured by gnawing or stripping bark, and by biting-off twigs and chewing them. The marmosets, possessing specialised incisor morphology for gouging holes in tree bark and directly stimulating the flow of exudate, may also consume gum and latex (Coimbra-Filho & Mittermeier, 1976, 1978; Ramirez *et al.*, 1978; Sussman & Kinzey, 1984; Stevenson & Rylands, 1988). Tamarins, lacking this specialised dentition, consume gum from a limited number of plant families opportunistically (e.g., *Anacardiaceae*, *Leguminosae*, *Combretaceae* and *Vochysiaceae*: Izawa, 1975, 1978; Garber, 1980, 1984b; Crandlemire-Sacco, 1986; Soini, 1987; Smith, 1997), relying upon either natural damage to bark or the parasitic activities of wood-boring insects, or both, in providing gum sites. However, at least two tamarin species are known to damage gum-producing plants when feeding to stimulate further exudate flow. These are *S. fuscicollis* (Soini, 1987) and *Leontopithecus rosalia* (golden lion tamarin) (Peres, 1989). *S. fuscicollis* is also known to exploit marmoset gum-feeding holes where it occurs syntopically with *Cebuella* (Soini, 1987) and *C. emiliae* (Ferrari & Martins, 1992). Available field data seem to indicate that *S. fuscicollis* is more gummivorous than most other tamarin species; a characteristic which is possibly related to its small size in relation to other tamarin species (Ferrari, 1993). Small body size is a correlate of gummivory in primates (Nash, 1986).

Plant exudates appear to be a seasonally-exploited food resource, many tamarins exploiting nectar from the flowers of *Combretum* or *Symphonia*, and gums from the elongate and fibrous pods of *Parkia* species, as alternative or keystone resources during the dry season when fruit production in the forest is generally low (Janson *et al.*, 1981;

Yoneda, 1984a, 1984b; Terborgh, 1983; Soini, 1987; Garber, 1988a; Buchanan-Smith, 1990a; Heymann, 1990a; Peres, 1991). In *S. fuscicollis*, however, gums may be consumed throughout the year (Garber, pers. obs.). Although small in variety, these alternative food sources make up a large percentage of foraging and feeding time during periods of scarcity (exudates and nectar can account for more than 50 % of total plant feeding time during a given two to three month period: Garber, 1980; Norconk, 1986; Soini, 1987; Ramirez, 1989).

Coimbra-Filho and Mittermeier (1977) have suggested that exudates provide tamarins with a high carbohydrate source not utilised intensively by other primates, nor by other mammals or birds. They may also provide some essential nutrients. For example, in addition to providing a source of non-structural complex polysaccharides, certain exudates are rich in calcium, which is often lacking in other parts of the tamarin diet and may be particularly important for reproductive females during pregnancy and lactation (Garber, 1993a). Floral nectar may serve as an alternative source of sugars, water (Baker & Baker, 1975; Freeman *et al.*, 1985), and to a lesser degree amino acids, proteins, lipids and vitamin C (Baker & Baker, 1975, 1983), during the potentially fruit-limited dry season. Garber (1988a) notes that the amount of these nutrients provided by individual flowers is

> *"likely to be small in comparison to the nutritional requirements of most other primate species, and therefore nectar-feeding activities are expected to include foraging patterns that reduce the costs of nectar acquisition and/or increase the quantity of the nectar reward"* (p. 103).

In a 12 month investigation of the foraging activities of a mixed-species troop of *S. fuscicollis* and *S. mystax*, he found that foraging activities associated with nectar feeding were reminiscent of traplining behaviour and were characterised by goal-directed travel to particular feeding areas. *S. fuscicollis* and *S. mystax* appeared to be aware of the distribution and location of flowering *S. globulifera* trees in their home range and to select nectar sites largely on the basis of proximity. Although *S. globulifera* exhibited a patchy distribution within the home range of the tamarin troop, the availability of nectar was highly predictable in space and time due to the population's floral synchrony. Based on this observation, Garber concluded that the tamarins probably retain a cognitive map of the spatial distribution of certain tree species in their home range and can assess the distance and direction from their present position to potential feeding sites. By minimising search costs through learning, memory and reduced travel, these small primates are able to forage efficiently, concentrating their feeding efforts on floral species of scattered distribution. However, although tree selection appears to be largely based on minimising the distance between feeding sites, expectations of the availability of the nectar reward were also found to influence foraging decisions. In many cases nearest-neighbour trees were probably selected because of the quantity of their food reward (i.e., preferred trees), irrespective of their proximity to the previous feeding tree. This led Garber to suggest that tamarins are probably even more dependent on a risk-sensitive foraging pattern than indicated in his analysis.

1.2.5 Ranging Patterns and Territorial Behaviour

Due to their small size, limited gut volume, and rapid rate of food passage (Crandlemire-Sacco, 1986; Garber, 1986), tamarins require a diet high in nutrient quality and available energy. As we have seen, this they obtain by feeding upon insects, ripe fruit, plant exudates and nectar. Although the natural availability of both insects and fruit is related to seasonal rainfall, the particular insects and fruit species taken by tamarins appear to provide them with the opportunity to exploit and defend delineated ranges throughout the year. The primary constituent of the insect component of the tamarin diet are orthopterans. For example, they are reported to comprise 61 % to 82 % of all identified animal prey for *S. fuscicollis* (Terborgh, 1983; Crandlemire-Sacco, 1986; Peres, 1993b). This is of critical importance, in that, in comparison to other insect forms, large orthopterans represent a relatively stable food resource due to their ability to survive prolonged dry periods in an adult stage of development, thereby constituting a high quality food source during what may otherwise be a food limited time of year. With regards to fruit, as described earlier, the main fruit species taken by tamarins ripen piecemeal over long periods of time. As such, fruit too constitutes a food resource assuring a reasonably long-term continuity of supply in time. This continuity appears to convey an advantage to tamarins in defending a delineated space for their exclusive use and hence they live in relatively rigidly-bound territories or home ranges (Terborgh, 1983). These are moderate to large at around 20 - 40 hectares (Garber, 1993a), although home ranges of over 100 hectares have been reported for mixed-species troops of *S. fuscicollis* and *S. imperator* at Manu National Park in Peru (Terborgh, 1983) and *S. fuscicollis* and *S. mystax* in Brazil (Peres, 1992a). Terborgh suggests that home ranges may be large at Manu because the tamarins there compete with nine other primate species and hundreds of bird species in what is the single most biodiverse protected area on Earth.

In all tamarin species for which quantitative data are available, mean day range generally exceeds 1200 metres (Garber, 1993a). Research suggests that the primary determinant of daily ranging patterns for primates is the distribution of available plant resources (Clutton-Brock & Harvey, 1977b, Oates, 1987). This appears to be the case for tamarins; circumstantial evidence (e.g., greater utilisation of parts of the home range near fruiting trees: Terborgh, 1983) suggests that patterns of movement and spatial utilisation in tamarins are controlled by the need to obtain fruit. Certainly, the relatively long distances travelled each day by tamarins appear to be more closely related to the distribution of plant resources than to invertebrate prey (Garber, 1993a). This makes intuitive sense, since insect resources are usually more evenly distributed than scattered and clumped plant resources, and thus insect foraging can be conducted during transit between fruiting trees. (Similarly, territory patrolling can at the same time serve an exploratory function in locating resources patches: Terborgh, 1983). Foraging time, however, appears constrained principally by the rate at which invertebrates are encountered and captured (Garber, 1993a).

So tamarins are highly territorial and expend a great deal of energy and time defending their home ranges aggressively against neighbouring troops (Neyman, 1978; Lindsay, 1979; Yoneda, 1981; Soini, 1982; Terborgh, 1983; Kinzey, 1986; Garber, 1988b; Snowdon & Soini, 1988; Buchanan-Smith, 1990a, 1991b; Peres, 1991). Home ranges are defended only against conspecifics, even when these are part of a mixed-species troop (Pook & Pook, 1982; Garber, 1988b; Buchanan-Smith, 1990a; Peres, 1992a). Aggressive troop-troop encounters occur near to the boundaries of their ranges and around important feeding trees (e.g., Garber, 1988b; Peres, 1992a), and may involve long-call vocalisations, movement towards the periphery of the range, and aggressive chases and displacements (e.g., Buchanan-Smith, 1991b). Not all inter-troop encounters are aggressive, however. This observation lead Buchanan-Smith (1991b) to suggest that, quite apart from their function in territory and resource defence, inter-troop encounters may help maintain or increase familiarity between neighbouring troops, thereby facilitating migration of individuals and the formation of new troops.

With increasing field research, it has become apparent that tamarin home ranges are not areas of exclusive use and adjacent ranges may overlap extensively. Furthermore, the degree to which neighbouring troops' home ranges overlap can vary greatly within species (e.g., less than 10 % overlap in *S. fuscicollis* at Manu: Terborgh & Goldizen, unpub. data; 79 % overlap between adjacent troops in *S. fuscicollis* at a Bolivian site: Yoneda, 1981). This does not mean that boundaries are unsettled, however, but rather that feeding sites located in areas of overlap are often exploited by more than one of neighbouring troop (there is much qualitative evidence to suggest that areas of home range overlap are frequently associated with major feeding trees, e.g., Crandlemire-Sacco, 1986, for *S. fuscicollis*; Dawson, 1976, 1979, for *S. geoffroyi*; Pook & Pook, 1982; Norconk, 1986; Garber, 1988b, for mixed troops of *S. fuscicollis* and *S. mystax*; Ramirez, 1989; Pruetz & Garber, 1991, for *S. mystax*). In this regard, tamarin home ranges have been described generally as a combination of shared overlap zones and exclusive territories (Norconk, 1986). Both areas, however, are defended in the presence of conspecific troops (e.g., Garber *et al.*, 1993b). Although the spatial relationship between food resources and inter-troop encounters has not been carefully mapped by researchers, Crandlemire-Sacco (1986) has suggested that, rather than defending territorial boundaries, it is fruit trees that are defended from neighbouring troops. In support of this view, Garber (1988b) reports a significant relationship between the location of major feeding sites and the location of inter-troop conflicts. He suggests that, given that these feeding sites generally produce only a small amount of ripe fruit each day, and are generally widely scattered throughout the troop's home range, first or priority of access is likely to be a critical factor in foraging success.

1.2.6 Locomotor and Postural Behaviour

Tamarins travel and forage mainly in the middle- to lower-canopy areas of the forest (Pook & Pook, 1982; Snowdon & Soini, 1988; Garber, 1991, 1992; Peres, 1991), an area containing many medium- to large-sized, horizontal and obliquely angled branches, upon which tamarins are able to locomote using quadrapedal progression (Fleagle & Mittermeier, 1980; Kinzey, 1986; Garber, 1991). The most common modes of locomotion are thus quadrapedal walking, running, bounding or galloping, combined with leaps, of which there are three types (Garber, 1991):

(1) Acrobatic leaps; these are used to cross large gaps in the forest canopy or for moving between adjacent tree crowns over a distance of 5 metres or more.

(2) Bounding leaps; these occur at the end of quadrapedal progression and are less than 2 metres in length.

(3) Trunk-to-trunk leaps; these are between medium- or large-sized vertical trunks in the forest understory and are usually between 1 and 2 metres in length.

In most tamarin species, the first two types of leaping dominate, but *S. fuscicollis* are unique in that they show an unusual amount of trunk-to-trunk leaping (Terborgh, 1983; Yoneda, 1984b; Soini, 1987; Buchanan-Smith, 1990a; Garber, 1991; Hardie, 1998). Amongst tamarin species, only *S. fuscicollis* appear to be predominantly adapted for the forest understory (Garber, 1991). This adaptation is crucial to the role that *S. fuscicollis* plays in its association with members of the *S. mystax* group, and is covered in more detail in Chapters 2 and 7.

The locomotion of the larger species is more fluid than that of the smaller (Hershkovitz, 1977). For example, *S. mystax* and *S. labiatus* locomote in a much less jerky and more feline manner than the smaller *S. fuscicollis* (Castro & Soini, 1978). When ascending and descending vertical boles and branches, a squirrel-like bounding is employed (Hershkovitz, 1977; Mittermeier, 1977; Prescott, pers. obs.). Standing, sitting, clinging and suspensory postures are used during feeding and foraging (Snowdon & Soini, 1988). Vertical clinging is used to cling to branches of relatively large diameter, particularly when feeding on exudate. With regards to this, Garber (1980, 1992) suggests that the 'claw-like' tegulae of tamarins represent a specialised adaptation for feeding on exudate, rather than a primitive character. Resting postures include sitting and lying on the stomach. During the heat of the day, tamarins relax by sprawling length-wise along a branch, their limbs and tails hanging free for maximum heat dissipation. Grooming is often seen at this time and is always performed in a sitting posture, with the recipient of the grooming sitting or lying upon its stomach, back or side (Snowdon & Soini, 1988).

One final point of interest concerning posture is the head-cocking seen commonly in tamarins, in which the head is rotated generally by 30 - 90° clockwise or anticlockwise (e.g., *S. fuscicollis*: Menzel & Menzel, 1980). This is a behaviour that has its function in improving visual, and quite probably auditory, perception in the three-dimensional sensory world of the forest (Snowdon & Soini, 1988). Callitrichines lack an ocular dominance column in their visual striate cortex, and head-cocking is thought to increase their ability to perceive depth, the head-cocking providing an effective increase in binocular disparity (Menzel, 1980). Head-cocks occur more readily in younger animals, are directed mainly towards novel objects as opposed to familiar ones, and habituate rapidly with continued exposure to the novel object (Menzel, 1980).

1.2.7 Sleeping Habits

All groups of all tamarin species observed, in the field or in captivity, pack themselves into a tight ball, limbs entwined, to sleep (Caine *et al.*, 1992). This huddling, along with a decreased night-time metabolic rate, may serve to minimise heat loss whilst enabling these small-sized animals to survive a 12 - 13 hour fast each night (sleep is profound in tamarins and usually lasts from sundown or dusk to sunrise) (Hershkovitz, 1977; Snowdon & Soini, 1988). Sleeping sites are usually tree holes, forks of branches, palms, or dense vine tangles (Moynihan, 1976; Terborgh, 1983; Yoneda, 1984a; Buchanan-Smith, 1989; Peres, 1991; Heymann, 1995). In addition to protection from the elements, such places are likely to provide safety from predators. When retiring to sleeping sites in the evening, tamarins employ a wide range of adaptations to reduce vulnerability to nocturnal predators, including careful selection of sleeping sites (Dawson, 1979, for *S. geoffroyi*; Neyman, 1978, for *S. oedipus*; Caine, 1990, for *S. labiatus*), increased vigilance (Caine, 1984, 1987, for *S. labiatus*), retirement before dusk (Yoneda, 1981, for mixed-species troops of *S. fuscicollis* and *S. labiatus*), reduced noise (Caine, 1987, for *S. labiatus*; Heymann, 1995, for mixed-species troops of *S. fuscicollis* and *S. mystax*), and torpor (Moynihan, 1970, for *S. geoffroyi*). Furthermore, Heymann (1995) suggests that sleeping in such closed places could reduce infection by dampening the diffusion of attractants to vectors, such as *Anopheles* mosquitoes, and thereby reducing overall exposure to them. Most troops appear to use several different sleeping sites, spread throughout their home ranges.

Detailed data on sleeping site use in mixed-species troops is only available for *S. fuscicollis* and *S. mystax* (Peres, 1991; Heymann, 1995). However, it would appear that, despite spending a considerable amount of their active time together, associating species in mixed-species troops nearly always separate during the course of the afternoon to make use of different sleeping sites. The distance between the species' sleeping sites varies. Heymann (1995) reports a range of 0 to 145 metres (with averages of 33 m and 40 m) for two different studies of associating *S. fuscicollis* and *S. mystax*. Peres (1991) reports a range of 15 to 120 metres (with an average of 46 m) for a mixed-species troop of the same species. Spatial proximity of sleeping sites is likely to be advantageous with regards rapid re-establishment of association early in the morning. This is achieved by long calls, initiated by either species. The sleeping sites of *S. fuscicollis* are consistently lower than those of *S. mystax* (e.g., modal heights of 9 - 12 m and 12 - 15 m, respectively: Heymann, 1995), reflecting the general vertical segregation seen between these species (see Section 2.4.2).

1.2.8 Communication

The Callitrichinae is one of the few primate subfamilies in which specialised sebaceous scent glands, variably concentrated in three epidermal regions (anogenital, suprapubic, and sternal), are used for communication. Indeed, the scent-marking behaviour of callitrichines is regarded as the most elaborately developed of all the simian primates (see Epple *et al.*, 1993, for a thorough review). Preference tests have revealed that a wide variety of information is coded in scent marks including species, subspecies, sex, individuality, social status, hormonal status and timing of ovulation (Epple, 1971, 1973, 1974a,b; Epple *et al.*, 1987; Ziegler *et al.*, 1993). Marking appears to have several functions including territorial defence (Epple, 1978a: *S. fuscicollis*), preparing males to assist in the delivery and care of new-born infants (Epple, 1975a: *S. fuscicollis*), and the reproductive suppression of subordinate females (Snowdon *et al.*, 1993, for *S. oedipus*). Odours are still effective up to three days after deposition (Epple *et al.*, 1980).

With regards to auditory communication, Snowdon and Soini (1988) write

"All callitrichids appear to use chirps or chuck-like sounds when foraging or being vigilant, trills when highly aroused, chevron-shaped mobbing calls, non-tonal calls for submission, and low frequency chatters when angry or afraid." (p. 277).

At least some species of tamarin also produce monitoring calls (also known as cohesion calls or contact calls) (e.g., Moody & Menzel, 1976, for *S. fuscicollis*; Caine & Stevens, 1990, for *S. labiatus*). According to Caine and Stevens (1990), these calls are given in no particular context and elicit no particular response, but rather allow individuals to keep track of the general whereabouts of their troop-mates, thereby maintaining intra-troop cohesiveness and permitting co-operative ventures (such as vigilance or transferring an infant). When palatable food is found, food calls are given which are thought to recruit troop-mates to the vicinity of the caller, probably for their anti-predatory vigilance benefit (Caine *et al.*, 1995, for *S. labiatus*). Long calls, which are in many ways functionally and ontogenetically similar to bird song, are given in territorial defence, to promote cohesion, to reunite separated troop members, and in mate attraction (Moynihan, 1970: *S. geoffroyi*; Snowdon *et al.*, 1983: *S. oedipus*). Tamarins are able to perceive the species-specificity (i.e, conspecific or congeneric caller) of long calls (Windfelder, 1997, for *S. fuscicollis* and *S. imperator*), as they are sex-specificity (Masataka, 1987, for *S. labiatus*). Pook and Pook (1982) suggest that the use of long calls for inter-specific communication is as least as important as their use in intra-specific communication (see also, Windfelder, 1997). In contrast to calls used in resting contact, which are low in both frequency and amplitude and are very short in duration, long calls and those calls given by isolated monkeys are louder in amplitude, longer in duration and contain more frequency modulation. All of these features increase the likelihood that a conspecific will locate the caller in the rapidly attenuating environment of the rain forest.

A number of authors have demonstrated that tamarins are able to subtly modify call structure to produce calls with different functions (Moody & Menzel, 1976; Cleveland & Snowdon, 1982; Snowdon *et al.*, 1983). For example, Moody and Menzel (1976) have differentiated between loud long calls and soft long calls in *S. fuscicollis*. The former being used for territorial defence and the latter for intra-troop cohesion. Furthermore, it has also been demonstrated, using playback experiments, that information concerning social situation or context can be communicated in the vocal signal alone (Snowdon *et al.*, 1983). At least two species of tamarin have different alarm calls for terrestrial and aerial predators (Epple, 1975a, for *S. fuscicollis*; Neyman, 1978, for *S. oedipus*) and species in mixed-species troops are known to respond to each others alarm calls (Buchanan-Smith, 1990a, for *S. fuscicollis* and *S. labiatus*; Heymann, 1987; Peres, 1993a, for *S. fuscicollis* and S. *mystax*; Terborgh, 1983; Windfelder, 1997, for *S. fuscicollis* and *S. imperator*).

Tamarins also communicate visually of course, but visual signals do not appear to play as great a role in tamarin behaviour as do chemical and auditory signals (Snowdon & Soini, 1988). This is, in part, due to the forest habitat which precludes transmission of visual signals over much of the day. Compared to the Old World monkeys and apes, the New World monkeys in general have poorly developed visual signals (Redican, 1975; Moynihan, 1976) and do not form the fine facial expressions seen in higher primates (Hershkovitz, 1977). There are a few visual signals in tamarins worthy of note. Tongue-flicking, used by many species, appears before copulation and in highly aggressive encounters and is thought to be unique to tamarins. Frowning is also common to most tamarins.

1.2.9 Colour Vision

The hallmark properties of primate vision are high spatial acuity and excellent discrimination of depth and distance (Jacobs, 1981). Moreover, their colour vision is quantitatively and qualitatively superior to that of all other mammalian groups (Jacobs, 1993; Jacobs *et al.*, 1996). However, unlike the catarrhines which, so far, have been found to have colour vision based on three classes of cone pigment (trichromacy), the platyrrhines are generally polymorphic in their colour vision. It is the case that, among all the diurnal platyrrhine species examined thus far, including *S. fuscicollis* (Jacobs *et al.*, 1987) and *S. mystax* (Boissinot *et al.*, 1997) but with the exception of *Alouatta* (howler monkeys), males may be one of three types of dichromat (i.e., all males are 'colour-blind') while females may be one of three types of dichromat or three types of trichromat. Given that the potential major advantage of trichromacy seems to be in the detection and identification of food, particularly ripe fruit in the dappled light of leaves (Polyak, 1957; Mollon, 1989, 1991; Osorio & Vorobyev, 1996; Regan *et al.*, 1996), dichromatic tamarins may be at a great disadvantage in their feeding, as emphasised by the fact that detecting fruit in trees is one of the rare tasks in which colour blind humans find especial difficulty (Steward & Cole, 1989). By relating genotypic data to behavioural data collected by myself, Buchanan-Smith *et al.* (unpubl. MS) have provided evidence that dichromatic *S. fuscicollis* and *S. labiatus* individuals are indeed at a disadvantage in their fruit detection and selection relative to trichromats.

Trichromatic individuals may not be at an advantage in all areas, however. For example, human dichromats can detect a perceptual organisation based on texture while the target is masked for normal trichromats by a rival organisation based on hue (Morgan *et al.*, 1992). Applying this to dichromatic monkeys in their natural habitat, they may be advantaged if they can detect camouflaged prey and predators missed by their trichromatic conspecifics (Mollon *et al.*, 1984).

Considerable behavioural variation between individuals within callitrichine troops has been reported elsewhere. For example, marked individual and sex differences have been found in vigilance (Caine, 1987; Goldizen, 1989; Savage, 1990; Price *et al.*, 1991; Buchanan-Smith, in press), in exploration of new territories (McGrew & McLuckie, 1986), in dispersal (Neyman, 1978) and feeding (Box *et al.*, 1995; Box, 1997). These may be related to the vision capabilities of the individuals involved. The application of genotype analysis may help in this regard, especially comparisons between dichromatic and trichromatic females alone (i.e., avoiding sex-based confounds). An appreciation of the particular colour vision phenotypes of captive study animals is important with regards appropriate experimental design. However, although this represents an under-explored area, it is beyond the scope of this thesis.

1.2.10 Conservation Status

Due to an almost complete lack of information on the populations of most of the callitrichines, decisions on conservation status are based almost entirely on the size of the geographic range and a gross overview of the state of destruction/development of the regions involved (Rylands *et al.*, 1993). *S. fuscicollis* is a forest species which can utilise secondary as well as primary forest (Hernández-Camacho & Cooper, 1976) and as such is able, in some areas (e.g., Peru), to maintain its populations well in areas of heavy forest degradation and live relatively unaffected by human disturbance (Freese *et al.*, 1978). In fact, logging and forest clearance provide an abundance of widely-differing spatial patterns of secondary forest which may actually favour tamarins in general (Rylands, 1996). However, the general global accelerated rate of deforestation is thought to be of potential threat to this species (Rylands *et al.*, 1993), together with heavy exportation for biomedical research and the pet trade (Freese *et al.*, 1978). *S. f. weddellii*, has the largest distribution of the *S. fuscicollis* subspecies, the largest part of which is in Bolivia where it was reported common in 1985 (Brown & Ruimz, 1986). A number of conservation units are within its geographical distribution.

The conservation status of *S. labiatus* is largely unknown. It appears that they are common in Bolivia, where until recently, numbers were enough to support commercial trapping for export in fairly large numbers (Heltne *et al.*, 1976; Cameron & Buchanan-Smith, 1992). In Brazil, *S. labiatus* is legally protected from commercial export (Mittermeier & Coimbra-Filho, 1977). A ban on the capture for export of all Bolivian primates expired in 1989 and the current situation is not known to the author. With regards the subspecies *S. l. labiatus*, Rylands *et al.* (1993) reported it as "*probably common throughout a large part of its range*" (p. 63). However, Encarnación (1990) reported that suitable habitat for *S. l. labiatus* was decreasing, drastically and rapidly, especially due to deforestation over the period 1987 to 1990, in the restricted region occupied by this species in Peru.

Having described the unusually stable associations formed between sympatric tamarin species, and having thoroughly reviewed the general behaviour and ecology of tamarins, we are now well placed to examine how and why they associate. The following chapter details the costs and benefits of association to individual tamarins in mixed-species troops.

Chapter 2

Costs and Benefits of Tamarin Mixed-Species Associations

"A genetic tendency to group with others and to interact with them in certain ways will, in the right circumstances, give the animals bearing it an advantage and their genes will spread."

[Manning & Dawkins, 1992: p. 150]

2.1 Introduction

A question that naturally arises from observations of animal associations is: what function do they serve? This is an interesting question because, all else being equal, grouping is assumed to involve a number of costs (see below). Most authors assume, at least implicitly, that associations occur because they provide benefits to the participants that outweigh any costs (i.e., individual animals that take part in associations are favoured via natural selection over those that do not), and thus attribute functional (adaptive) advantages to such associations. However, it should be noted that the costs and benefits of association may be different for different individuals and, in polyspecific associations, may be asymmetrical between species.

What follows in this chapter is a detailed examination of the potential costs and benefits of association in primates in general and in tamarin mixed-species associations in particular. I begin by describing the potential costs first, and then the benefits, and for each, I indicate whether there is evidence they are accrued in tamarin mixed-species troops. Many of the benefits described for primate mixed-species troops are simply a consequence of increased troop size. Mixed-species troops of tamarins, however, may accrue additional benefits, as a result of species divergence in behaviour and as a consequence of their mating system. These additional benefits make mixed-species tamarin troops advantageous over similarly-sized single-species ones and are discussed in the following section. Next, I discuss asymmetry in the costs and benefits accrued to different species and different individuals in tamarin mixed-species troops. I then describe the factors controlling troop size in tamarin mixed-species troops. Lastly, I elaborate upon the aims of the thesis.

2.2 Costs of Associating

Potential costs proposed for primate associations are largely a consequence of increased troop size and include increased feeding competition (e.g., Gautier-Hion, 1980; Terborgh, 1983), increased conspicuity (e.g., Gautier-Hion & Gautier, 1974; Heymann & Buchanan-Smith, submitted) and increased parasitism (e.g., Freeland, 1977). Investigations of the costs of association in tamarin mixed-species troops have received less attention than the benefits. The main costs proposed are increased feeding competition and those costs associated with maintenance of the association (although all the other costs mentioned above may apply).

2.2.1 Increased Feeding Competition

For primates, grouping is generally assumed to result in an increase in feeding competition among troop members (Altmann, 1974; Wrangham, 1980, 1987; van Schaik, 1983; Dunbar, 1988; Janson, 1988; Janson & van Schaik, 1988; Symington, 1988). Alexander (1974) has gone so far as to say that increased feeding competition is an ‘automatic’ and ‘universal’ consequence of grouping. Synchronisation of feeding activity tends to increase *interference competition* (direct aggressive interaction between competitors for food items), and the joint use of common resources in a given area increases *exploitative competition* (competitors denying one another access to a common resource supply by directly depleting it, but without directly meeting). However, although competitive inequalities can play a role in group dynamics, competition is not necessarily automatic (Rubenstein, 1978). It is only a problem if resources are limiting and, in polyspecific groups, if the species in question are potential competitors. So, we are left with the question: does inter-specific competition for food occur between associating primate species? Its occurrence has most often been inferred based on habitat or diet partitioning (Gartlan & Struhsaker, 1972; Struhsaker, 1978; Fleagle *et al.*, 1981; Pook & Pook, 1982), and although interference competition has been observed directly (Gartlan & Struhsaker, 1972; Klein & Klein, 1973; Struhsaker, 1981), some authors regard exploitative competition as perhaps more important than interference competition in primates (Waser & Case, 1981). In fact, because evidence is largely anecdotal, the role of competition in primate mixed-species troops is difficult to evaluate. However, most studies of primate mixed-species troops conclude that competition is not actually exacerbated in them, either because no inter-specific aggression was observed (Bernstein, 1967; Gautier & Gautier-Hion, 1969; Gautier-Hion & Gautier, 1974) or because the food eaten by the mixed-species troops was judged to be superabundant (e.g., Gartlan & Struhsaker, 1972).

With regards to mixed-species troops of tamarins, given that overlap in the plant portion of the diet can be extensive between the participating species (e.g. Terborgh, 1983; Garber, 1986, 1988b, 1993a,b; Ramirez, 1989; Buchanan-Smith, 1990a; Hardie, 1998), it does not seem logical that they should co-exist when they must surely be competing for the same resources. Moreover, in all tamarin mixed-species troops studied thus far, *S. fuscicollis* are subordinate to their larger congeners, and are sometimes displaced from small, monopolisable feeding trees by them (e.g., Terborgh, 1983; Heymann, 1990a; Peres, 1996; Hardie, 1998). The cost of increased feeding competition may thus be greater for *S. fuscicollis* than for their congeners. However, the cost to either species may not be a large one as the majority of the plant food resources consumed by tamarins in mixed-species troops are comprised of large (relative to the monkeys themselves), non-monopolisable trees (Pook & Pook, 1982; Garber, 1993a; Peres, 1993b). At such trees, both species feed together in the same tree or occasionally in neighbouring trees (i.e., feed in parallel), or *S. fuscicollis* may enter a tree as their congeners exit (i.e., feed in series), suggesting little feeding competition between them. In fact, most studies report little agonism (interference competition) between associating tamarin species (Pook & Pook, 1982; Peres, 1993b; Buchanan-Smith, 1990a; Heymann, 1990a). In addition, in all tamarin mixed-species troops studied to date there is vertical segregation between the associating species, with *S. fuscicollis* occupying lower heights in the forest than their congeners (Yoneda, 1981, 1984a; Pook & Pook, 1982; Terborgh, 1983; Norconk, 1986, 1990b; Buchanan-Smith, 1999; Peres, 1992a,b 1996). This may act as a spacing mechanism to reduce inter-specific feeding competition (Heymann & Buchanan-Smith, submitted). Feeding competition between associating tamarin species appears to be reduced also because of divergence in the type of insect prey consumed (e.g., Terborgh, 1983; Norconk, 1990b; Peres, 1992b). For example, it has been shown that the size and class of insect prey consumed by *S. fuscicollis* and *S. mystax* does not overlap greatly, and that few inter-specific aggressive interactions occur whilst insect foraging (Peres, 1992b; Nickle & Heymann, 1996). The implications these divergences in ecological niche have on mixed-species troop formation will be discussed in more detail later in this chapter and in Chapter 7.

At present there is only one documented case of a potential feeding cost to a resident tamarin species of forming a mixed-species troop. Terborgh (1983) reported *S.*

imperator travelled a greater distance per day when in association with *S. fuscicollis* than when alone, although, during this time neither species exhibited any change in the number of trees visited per hour. He suggested that, as a result of the exploitative competition on the part of *S. fuscicollis*, *S. imperator* have to travel farther to find the next resource. In contrast, in a study on the feeding ecology of a mixed-species troop of *S. fuscicollis* and *S. mystax*, Garber (1988b) found no evidence that changes in troop size (i.e., an increase in the number of *S. mystax*) had any significant effect on day range, dietary preference, activity budget, or number of daily feeding bouts of either resident species. This led Garber to conclude that despite extreme dietary overlap, feeding competition within the troop was minimal and outweighed by advantages associated with co-operative territorial and resource defence. In general, the available evidence suggests that inter-specific feeding competition does not place high demands on the participants of tamarin mixed-species troops.

2.2.2 Maintenance Costs

Aside from possible feeding competition, associating tamarins are also likely to incur maintenance costs as a result of activities such as antiphonal long calling (i.e., alternate long calling between species) to establish and maintain contact (Pook & Pook, 1982; Heymann, 1990a; Peres, 1991); backtracking when separated (Pook & Pook, 1982; Terborgh, 1983; Buchanan-Smith, 1989); and choosing sleeping sites relatively close to one another (Peres, 1991; Heymann, 1995). Such activities are likely to increase energetic expenditure and may also increase conspicuity, alerting potential predators. In all tamarin mixed-species troops studied thus far, both species participate in the maintenance of the association (Terborgh, 1983; Buchanan-Smith, 1990a; Norconk, 1990b) and thus these costs are likely to be borne by both species.

2.3 Benefits of Associating

The functional explanations proposed for tamarin mixed-species associations are similar to those proposed for intra-specific gregariousness in animals in general and fall within three broad categories:

(1) those related to decreasing the risk of predation;

(2) those related to increasing foraging success;

(3) those related to increasing the ability to defend resources.

2.3.1 Decreased Risk of Predation

One of the major arguments advanced for the evolution of large social troops is to decrease the risk of predation (e.g., Terborgh & Janson, 1983; van Schaik, 1983). Through the aggregate behaviour of their members, large troops can effectively foil the efforts of predators in a variety of ways:

(a) More eyes and ears:

Large troops have more eyes and ears available to detect predators, promoting earlier detection (e.g., van Schaik, 1983). This advantage applies equally well to mixed-species troops as a consequence of mixed-species troop formation is an increase in troop size. The efficacy of this mechanism depends upon the transmission of warning signals between troop members. In this regard, participating species in tamarin mixed-species troops are vulnerable to a common set of predators (e.g., Terborgh, 1983; Heymann, 1987, 1990b; Buchanan-Smith, 1990a) and are known to respond to each others alarm calls (Buchanan-Smith, 1990a, for *S. fuscicollis* and *S. labiatus*; Heymann, 1987; Peres, 1993a, for *S. fuscicollis* and *S. mystax*; Terborgh, 1983; Windfelder, 1997, for *S. fuscicollis* and *S. imperator*).

Also by augmenting the number of attentive eyes and ears, increased troop size may allow *individuals* to spend less time being vigilant (Gartlan & Struhsaker, 1972; Rudran, 1978; Struhsaker, 1981; Pook & Pook, 1982; Gautier-Hion *et al.*, 1983; Cords, 1990; Hardie & Buchanan-Smith, 1997). Hardie and Buchanan-Smith (1997) have demonstrated that, in captive troops of *S. fuscicollis* and *S. labiatus*, for both species, the mean amount of time each individual spends in vigilance is less in mixed-species troops than in single-species troops. Moreover, despite this decrease in individual vigilance in mixed-species troops, detection of predators by the mixed-troop as a whole (overall vigilance) is increased (there were fewer times when no animal in the mixed-species troops was vigilant), relative to single-species troops. Such a decrease in individual vigilance behaviour afforded by association may, in turn, allow more time for other important activities such as foraging, since vigilance is incompatible with searching micro-habitats for insects and, to some extent, selecting and processing fruit (Hardie & Buchanan-Smith, 1997). This hypothesis has been tested empirically only in single-species flocks of birds (e.g., Caraco, 1979; Caraco *et al.*, 1980b), although Buchanan-Smith (in press) found that captive *S. fuscicollis* and *S. labiatus* engaged in significantly more foraging in mixed-species troops than in single-species troops. The findings of Hardie and Buchanan-Smith demonstrate that, in mixed-species troops of *S. fuscicollis* and *S. labiatus*, individuals of both species alter their rates of vigilance in response to the presence of the other species. The advantages accrued to individuals are not specific to mixed-species troops *per se* but are simply a consequence of increased troop size. However, tamarin mixed-species troops may gain additional anti-predatory advantages over single-species troops. These are described later.

(b) Confusion:

Mixed-species troops may deter a predator's attack by confusing the predator; the increased number of individuals in the mixed-species troop and their resultant unpredictable, evasive movement (fleeing with intersecting pathways) make it more difficult for the predator to single out and track a target prey animal (Curio, 1976; Kiltie, 1981; Struhsaker, 1981; Landeau & Terborgh, 1986). Confusion of the predator has been demonstrated experimentally to reduce predation success rates by *Loligo vulgaris* (squid), *Sepia officinalis* (cuttlefish), *Esox lucius* (pike), and *Perca fluviatilis* (perch) (Neill & Cullen, 1974). However, it should be noted that the prey animals themselves can also become confused, become separated, or collide with one another and find their escape impeded.

(c) Mobbing:

Primates are often not just passive victims of predation and owing to the increased number of individuals in mixed-species troops, their members may be able to defend themselves against the unwelcome attentions of a predator more effectively (Gautier-Hion & Tutin, 1988). In fact, co-operative troop defence against, and mobbing of, potential predators has been reported quite often for primates (e.g., Crook & Gartlan, 1966; Stoltz & Saayman, 1970; Eisenberg *et al.*, 1972), including callitrichines (Bartecki & Heymann, 1987; Ferrari & Lopes Ferrari, 1990a). Mixed-species troops of *S. fuscicollis* and *S. labiatus* have been observed to jointly mob *Eira barbara* (tayra), a stoat-like mustelid

(Buchanan-Smith, 1990a), as have mixed-species troops of *S. fuscicollis* and *S. mystax* (Peres, 1991).

(d) Selfish-herd:

Mixed-species troops may be selfish-herds, such that each prey individual tries to position another prey individual between itself and the predator and effectively use that individual as a living shield (Hamilton, 1971; Vine, 1971). Moreover, if, by virtue of higher dominance rank, some 'selfish' individuals (or species) were able to consistently maintain positions near the centre of the troop, they would gain an increased measure of safety at the expense of those forced to take positions at the periphery (Terborgh, 1990). In the association between *Colobus badius* (red colobus) and *Cercopithecus diana* (Diana monkey), *C. badius* are found higher in the forest canopy than *C. diana*. According to Hoelenweg *et al.* (1996), it is possible that *C. badius* use *C. diana* as a shield against *Pan troglodytes* (common chimpanzee) attacking from below, and *C. diana* use *C. badius* against *Stephanoaetus coronatus* (crowned eagle) attacking from above.

(e) Dilution:

Finally, mixed-species troops may dilute the successful predator's effect, in that, statistically, the more potential prey individuals there are present, the less likely it is that any one individual will be the unfortunate victim (Terborgh, 1986; Waser, 1987; Bertram, 1978). This is often termed 'safety in numbers'. If all prey individuals are capable of taking evasive action, and if the predator can kill only one prey individual per successful attack, then in the event of an attack, the probability that any particular individual is the target victim is $^1\!/_N$, where N is the number of individuals in the troop. As N increases, the derived anti-predatory benefit increases also, rapidly at first, and then ever more slowly, but without limit (Terborgh, 1990). To some extent this dilution effect may be offset by an increased number of attacks on larger and more conspicuous groups, but in general, for animals capable of escaping from their predators, the increased collective ability to detect the predator in large groups probably exceeds their disadvantage due to increased conspicuity (Vine, 1971; Treisman, 1975a,b).

Rates of observed predation in primates are so low that the importance of these anti-predatory benefits for primate mixed-species associations is generally argued on inference (e.g., Gautier-Hion *et al.*, 1983; van Schaik, 1983; Pulliam & Caraco, 1984; de Ruiter, 1986; Stacey, 1986). This has been the case for tamarin mixed-species associations (Terborgh, 1986; Windfelder, 1997) and in criticism of this approach Garber (1988b) writes that

> *"in the absence of more detailed information, it is premature to speculate on the effects that predators have on tamarin social organisation, and whether individuals in larger groups are significantly less at risk than those in smaller groups"* (p. 29)

However, the infrequency of successful predatory attempts does not mean that predation risk is insignificant, and although the role of predation in determining mixed-species association remains largely unsubstantiated for primates, it is potentially important (Cords, 1987). Predators are ubiquitous in the species-rich habitats of tamarins and it has been suggested that tamarins have the highest rate of predation of all primates (Cheney & Wrangham, 1987). Due to their small size, they are potentially vulnerable to a wide range of predatory birds, reptiles and mammals (Hershkovitz, 1977; Neymann, 1978; Izawa, 1978; Dawson, 1979; Terborgh, 1983; Emmons, 1987; Heymann, 1987, 1990b; Buchanan-

Smith, 1990a), although it appears that medium- to large-sized diurnal raptors present the greatest predatory threat (Terborgh, 1983; Sussman & Kinzey, 1984; Goldizen, 1987b; Heymann, 1990b; Peres, 1993a). For example, Goldizen (1987b) reports one raptor attack per week per tamarin troop at Manu National Park, Peru, and Heymann (1990b) observed alarm events every 2 to 3 hours for three mixed-species troops of *S. fuscicollis* and *S. mystax* at Río Blanco, Peru, half of which were to raptors. Anecdotal reports of tamarin predation include aerial attacks by *Spizaetus ornatus* (ornate hawk-eagle) (Terborgh, 1983; Heymann, 1990b), *Accipiter bicolor* (bicoloured hawk) (Terborgh, 1983), *Micrastur ruficollis* (barred forest-falcon) (Izawa, 1978) and *Daptrius americanus* (red-throated caracara) (Ramirez, 1989); and terrestrial attacks by the *Felis pardalis* (ocelot) (Heymann, 1990b), *Eira barbara* (Smith, pers. comm. to Moynihan, 1970; Jansen, pers. comm. to Galef *et al.*, 1976; Ramirez, 1989; Buchanan-Smith, 1990a), and *Eunectes murinus* (anaconda) (Heymann, 1987).

Predator behaviour is strongly habitat dependent (Curio, 1976) and in the closed habitat of the tropical rain forest, where visibility is poor and impediments are posed by vegetation, predators must wait in ambush or employ stealthy stalking in order to come within striking distance of their prey. Under these circumstances (attack at close range) the prey is given little warning and even an instant's advance notice may mean the difference between death and escape. Early warning alarm signals are thus at a premium and such anti-predatory benefits may have provided a strong incentive for association (Terborgh, 1990) or sociality (Caine, 1993) in tamarin troops.

Buchanan-Smith and Hardie (1997) argue that, if mixed-species association does decrease predation rates in tamarins, it is likely to be through improved early detection and avoidance of predators, rather than any other mechanism such as confusion or mobbing. As noted by Terborgh (1990), the confusion effect operates under the limitation that prey must be fully visible to the predator and under pursuit for some distance. In the closed confines of dense vegetation, where tamarins spend much of their time, these conditions are seldom met and it is consequently unlikely that tamarins will be able to confuse predators by fleeing in concert. Moreover, in response to aerial predators, tamarins appear to rely more on crypsis (i.e, remaining immobile, hiding beneath foliage), retreating from the periphery of a tree to the tree trunk, or most dramatically, dropping to the ground (e.g., Caine, 1987; Dawson, 1979; Heymann, 1990b; Peres, 1991). With regards to mobbing Bartecki and Heymann (1987) suggest that, given the small size of tamarins, mobbing is likely to be relatively ineffectual as a deterrent. Instead, they propose that its adaptive significance lies in informing the predator, whose success often depends upon surprise, that they are aware of its presence, or else in the cultural transmission of information about potential predators to other troop members. It is known that intense emotional responses to predators can lead to conspecifics learning those same responses (observational conditioning) (e.g., Mineka & Cook, 1993, for observational conditioning of snake fear in *Macaca mulatta* (rhesus macaque)). Finally, the vertical segregation observed in tamarin mixed-species troops does not lead to optimum conditions for the selfish-herd effect, or for dilution, because the species are separated.

2.3.2 Increased Foraging Efficiency

In addition to possible benefits in reducing predation, association in mixed-species troops may facilitate the task of food finding and its subsequent utilisation, thereby increasing foraging efficiency. It may do this in a number of ways, most of which require dietary similarity between associating species in order to be applicable. Data on feeding show that the diets of associating tamarin species overlap substantially in their plant food component (Buchanan-Smith, 1990a; Hardie, 1998, for *S. fuscicollis* and *S. labiatus*; Norconk, 1986; Garber, 1988b; Ramirez, 1989; Castro, 1991; Peres, 1993b, 1996, for *S. fuscicollis* and *S. mystax*; Terborgh, 1983, for *S. fuscicollis* and *S. imperator*).

(a) Sharing or parasitism of knowledge:

Decisions governing foraging in large troops may be more efficient because sources of information are better and more numerous, owing to the increased number of individuals (Gautier-Hion *et al.*, 1983). If individuals are able to capitalise upon the skills and knowledge of more experienced troop members through social learning, then access to a larger knowledge base will be an advantage of mixed-species troops and large single-species ones. This hypothesis is considered in greater detail in Section 3.4.

Related to this hypothesis is the proposition that associating species in mixed-species troops can capitalise upon distinct facets of behaviour which are species-specific but may additionally give advantage to the associating species, for example, differential responses to novel stimuli or situations (*S. fuscicollis* and *S. labiatus*: Buchanan-Smith, 1989, for baited traps in the forest; Hardie, 1995, for novel objects), or to predators (*S. fuscicollis* and *S. mystax*: Bartecki & Heymann, 1987; Heymann, 1990b; Norconk, 1990b; Peres, 1991, 1993b). Increased opportunity for social learning, owing to the increased number of individuals in mixed-species troops, along with the opportunity to learn from the species-divergent behaviour of congeners, represents the main foraging benefit hypothesis explored in this thesis.

That associating tamarin species can learn from one another about the presence of food has been confirmed in captive studies. For example, Hardie (1995) demonstrated that in single-species troops, *S. fuscicollis* and *S. labiatus* individuals would contact objects which they had not learnt to pair with food significantly fewer times than when the same objects were presented in a mixed-species troop and their congeners had learnt to pair the object with food. Both species were clearly sensitive to the presence and behaviour of their congeners, which facilitated their approach responses to the objects paired with food.

(b) By forming associations, species gain access to otherwise unavailable food:

In the associations formed between *Saimiri sciureus* (common squirrel monkey) and *Cebus apella* (black-capped capuchin), the *Saimiri* are able to scavenge partially eaten *Scheelea* nuts dropped by the *Cebus*; nuts that, being large and tough, are ordinarily inaccessible to the former (Terborgh, 1983). Similarly, species in mixed-species troops may increase their prey capture rates by feeding on insects or other such prey items flushed from hiding places by their congeners (Gartlan & Struhsaker, 1972; Klein & Klein, 1973; Gautier-Hion & Gautier, 1974; Gautier-Hion, 1978; Rudran, 1978; Munn & Terborgh, 1980; Pook & Pook, 1982; Waser, 1982). Terborgh (1983) argues that this effect is likely to be more relevant to mixed-species bird flocks than to primate mixed-species troops since the kind of insects that would be flushed are best caught by stealth and surprise, unless the predator is able to capture them in the air as they flee. However, Peres (1992b) has since described *S. mystax* flushing insects (large orthopterans) to lower substrates which facilitates their capture by *S. fuscicollis*. The typically anti-predatory response of many orthopteran prey when disturbed, is to leap or fall away rapidly to a new position. The efficiency of this strategy (for the insects) is obviously greatly reduced at low levels in the forest since further escape is virtually impossible once the insect reaches the ground. *S. fuscicollis* are far more willing than their congeners to descend to the forest floor (Buchanan-Smith, 1989; Heymann, pers. obs.) and Peres (1992b) reports that *S. fuscicollis* more than doubled their insect prey yield by foraging alongside *S. mystax* and capturing the prey items flushed downward by this species from the lower and middle canopy areas of the forest. The retrieval of flushed prey by *S. fuscicollis* appears to incur little or no cost to *S. mystax* because prey items diving for cover become largely inaccessible both to the flusher and its conspecifics (i.e., they were ones they would not catch anyway). Given that animal prey represents the highest quality dietary component of wild tamarins, and that over 70 % of the prey biomass harvested by *S. fuscicollis* was flushed prey, the opportunity to exploit such prey may be a major incentive for *S. fuscicollis* to associate (Peres, 1992b). As stated earlier, *S. fuscicollis* may also achieve access to otherwise unavailable food in its association with *C. emiliae*; exploiting gum produced by the gouging activity of the latter (Lopes & Ferrari, 1994).

(c) One species may act as a guide to its congener:

The ability of one species to find food may be enhanced by another species serving as a guide to temporarily abundant food (Moynihan, 1970; Rudran, 1978; Gartlan & Struhsaker, 1972; Struhsaker, 1981; Pook & Pook, 1982; Skorupa, 1983; Terborgh, 1983; Cords, 1987). However, the hypothesis that one species, better informed about the location and quality (in terms of abundance and ripeness) of resources, serves as a guide to high quality feeding sites is difficult to disprove and requires detailed information on the feeding efficiency, relative to ranging, of the guided species.

Inequality of knowledge about the location of food resources is likely when the home ranges of associating species are substantially different in size. The species occupying the larger home range may benefit from the superior, intimate knowledge of resource availability of the species occupying the smaller range by using them as guides to resources within the shared area. This appears to be the case in some cercopithecine mixed-species troops (Gartlan & Struhsaker, 1972; Rudran, 1978; Struhsaker, 1981; Cords, 1990) and in associations between *S. sciureus* and *C. apella* (Terborgh, 1983; Podolsky, 1990). Such a benefit may also apply to the association of *Callimico* with tamarin species, but given that associating tamarin species have almost completely overlapping home ranges, inequality between the tamarin species themselves, concerning the location of resources, is unlikely. Nevertheless, guiding may apply to resources located at different heights. Peres (1996) has shown that *S. mystax* more often encounter large, productive food patches located higher in the forest (trees that can accommodate the whole mixed-species troop), whereas *S. fuscicollis* more often encounter smaller food patches, lower in the forest, from which they are often displaced by the dominant *S. mystax*. However, while these findings suggest some degree of inequality of knowledge, it is still possible that both species know about the location of the patches. In fact, Terborgh (1983) reports that, in mixed-species troops of *S. fuscicollis* and *S. imperator*, *S. fuscicollis* run ahead of *S. imperator* and arrive first at the best feeding trees (which are more likely to be the large productive patches) implying that both species know of their location. Other researchers have found that the members of the *S. mystax* group lead *S. fuscicollis* to the position of large feeding trees (Buchanan-Smith, 1989, 1990a; Peres, 1996).

(d) Associating species might exploit food more systematically and thus more efficiently:

It has been suggested that mixed-species troops may reduce their search time for food by avoiding duplication of effort (i.e., minimising the frequency of path re-crossing) and by regulating their return time to renewing resources, as proposed originally by Cody (1971) for mixed-species finch flocks in the Mojave Desert, California. The idea is that, by banding together, troops of one species can ensure that they do not visit fruit resources that troops of another species, with which it shares its home range, have recently exploited, and which are thus unlikely to contain ripe fruits (Gautier-Hion *et al.*, 1983; Cords, 1987, for cercopithecines). Such a mechanism could either save the energetic expenses of travel to unprofitable trees, and/or reduce the risk of predation incurred by extra travel. All species thereby avoid a duplication, or multiplication, of effort. Furthermore, the co-ordinated use of feeding trees by species in mixed-species troops enables individuals to regulate their return times to continuously renewing resources (e.g., nectar) or to ripening resources (fruit) more efficiently, and thereby maximise food renewal (yield) between visits (Whitesides, 1981; Terborgh, 1983; Cords, 1987).

Cody's (1971) renewing-resource model has been questioned because of its extreme sensitivity to some of its numerical assumptions (Pyke *et al.*, 1977). For example, in the model, Cody simulated the movements of his finch flocks on a grid of 11 x 11 points with a reflecting boundary (i.e., when the boundary was hit, the next movement was assumed to be backwards). Most animals, however, probably do not treat the boundaries of their foraging areas as reflecting boundaries (e.g. Pyke, 1974). Furthermore, the model assumes that animals move independently of the presence of food at distant localities. Most animals, however, probably do detect and respond to food at a distance. Nevertheless, the question remains: are there conditions under which a species foraging with competitors saves enough search time to outweigh its pre-emption from some food resources? Waser (1987) writes that a formal analysis of this possibility for primates, like that of Clark and Mangel (1984) for flocking birds, would be desirable. On the strength of a number of simple models, Clark and Mangel found that, as a result of sharing information and the food finds of others, group foraging can increase mean individual feeding rates and furthermore, may reduce variance in these feeding rates. Such a mechanism has been postulated for *S. fuscicollis* and *S. mystax* in Peru by Terborgh (1983). Terborgh suggests that, by travelling together the two species are potentially able to monitor the feeding activities of the other, and thereby avoid futile visits to trees that have already been exploited. In this way they can enhance their realised foraging efficiency (whilst reducing their mutual competitive interaction by choosing separate but nearby feeding trees). A further potential benefit could be gained by regulating return times to particular trees or portions of their territory in order to maximise the yield on each visit. However, several authors have noted that, in areas where troops are characterised by home range overlap, this particular foraging strategy is only effective if feeding sites are actively defended against neighbouring troops so that there is no interference by them with the renewal pattern (Hamilton *et al.*, 1976, for *Papio ursinus* (Chacma baboon); Stacey, 1986, for *Papio cynocephalus* (yellow baboon)). Garber (1988b) proposes that mixed-species troops of *S. fuscicollis* and *S. mystax* do just that, and argues that associating species in mixed-species troops can monitor, defend and exploit productive feeding trees from neighbouring mixed species troops more efficiently than they could alone. He writes that, for mixed troops of *S. fuscicollis* and *S. mystax*

> *"the relative costs of a co-ordinated feeding effort and co-operative resource defence are likely to be small in comparison to the costs to individuals in each group of monitoring and defending feeding sites separately"* (p. 31).

The advantages to be realised in avoiding redundant visits depends critically upon the characteristics of the resource in question. They would be minimal for large, synchronously ripening (non-renewing) fruit crops, and maximal for small, slowly ripening (self-renewing) crops that are relatively little exploited by other (third party) species. The major fruit resources of tamarins do indeed conform to the latter set of characteristics, being generally characterised by small to moderate-sized crowns (Terborgh, 1983, 1986), a high degree of intra-specific fruiting synchrony, and the production of small amounts of ripe fruit each day (Terborgh, 1983, 1986; Crandlemire-Sacco, 1986; Garber, 1986, 1988b; Soini, 1987). However, due to the difficulty of collecting relevant data, this foraging benefit hypothesis has not yet been properly tested in wild tamarin mixed-species troops.

2.3.3 Increased Ability to Defend Resources

Resource defence benefits can be derived in mixed-species groups if the two (or more) associating species together have a greater inter-group competitive ability than monospecific groups (Munn & Terborgh, 1980). In several callitrichine species, there is evidence that neighbouring troops compete for access to productive feeding trees located in shared areas of their range (Dawson, 1979; Crandlemire-Sacco, 1986; Peres, 1986a; Rylands, 1986b; Garber, 1988b; Stevenson & Rylands, 1988; Ramirez, 1989). Garber *et al.* (1993b) suggest that the ability of a troop to dominate its neighbour at these feeding sites is likely to be a critical factor in foraging success. An increase in troop size, as a result of mixed-species troop formation, is thought to increase the ability of associating primate species to jointly defend *shared* food resources and to defend a territory (and hence the food resources within it) against neighbouring troops, thereby increasing the longevity of territory ownership (Gautier-Hion *et al.*, 1983; Soini & Soini, 1983; Terborgh, 1983;

Norconk, 1986; Waser, 1987; Garber, 1988b; Ramirez, 1989; Peres, 1992a). This may, in turn, result in higher reproductive rates for those individuals participating in mixed-species troops compared to those in single-species troops (Norconk, 1990b), although this (long term benefit) remains to be tested. As mentioned earlier, Garber (1988b) suggests that aggressive inter-troop encounters between mixed-species of tamarins are related to resource defence and they are thought by him to be one of the most critical factors maintaining the association between *S. fuscicollis* and *S. mystax*. He suggests that such mixed-species troops are able to monitor, exploit and defend productive feeding trees from neighbouring troops more easily than could the participating species alone. By comparing resource defence in a mixed-species troop which varied in size, he demonstrated a positive relationship between the size of the mixed-species troop and the ability of the troop to defend major feeding trees successfully (the cost to the smaller troop was increased travel and lower foraging efficiency). However, because the increase in troop size was a result of an increase in the number of *S. mystax* only (the number of *S. fuscicollis* remained constant), it maybe that the competitive ability of *S. mystax* alone, rather than the combined ability of *S. mystax* and *S. fuscicollis*, was the pertinent factor in increasing the ability to defend the resources.

2.4 Additional Benefits to Tamarins in Mixed-Species Troops

As we have now seen, the selective benefit hypotheses proposed for polyspecific associations in primates are largely the same as those used to explain intra-specific gregariousness, assuming that predators and diet are common to the different associating species. However, although any or all of the above hypotheses may operate in mixed-species troops, it is sometimes not clear why selection does not simply favour large monospecific troops, rather than the association of two or more different species. The pertinent question is: why is it that individuals in mixed-species troops are better (or at least no worse) than individuals in similarly-sized single-species troops at performing these functions? For mixed-species troops of tamarins there are a number of possible answers.

2.4.1 Divergence in Insect Foraging

Differences in resource utilisation and dietary requirements are generally greater between species than within species (Morse, 1980). In areas where resources are scarce, the formation of a mixed-species troop is thus likely to result in less intense feeding competition than the formation of a similarly-sized monospecific troop. That is, grouping benefits and intra-specific competition are diametrically opposed at the single-species level but this can be alleviated, at least partially, if troops can associate with another species that does not totally compete for resources (Peres, 1991, 1993b). Peres (1993b) writes

> *"Combining with conspecifics to form yet larger groups may...be prevented by ecological and behavioural thresholds limiting the size of monospecific groups, such as local feeding competition and intrasexual aggression towards reproductive competitors. Animals may then associate with those of another species that is ecologically similar [which may be compatible with respect to foraging] to avoid common predators whilst minimizing competition for food and mates."* (p. 61).

Tamarin species in all mixed-species troops have been observed to forage on different insect prey utilising different insect foraging methods. For example, Terborgh (1983) reports *S. fuscicollis* foraging primarily by investigating knotholes and crevices on trunks and branches for mostly large (25 - 50 mm), cryptic prey, 80 % of which are hidden before capture. In contrast, *S. imperator* does most of its insect foraging on leaves and, although *S. imperator*'s prey are roughly the same size as those of *S. fuscicollis*, they are much more mobile and 79 % are exposed prior to capture. *S. labiatus* and *S. mystax* have been found by other authors to exhibit a similar pattern to *S. imperator* (e.g., Buchanan-Smith, 1990a; Yoneda, 1981, 1984a, for *S. labiatus*; Garber, 1988b; Peres, 1992a, for *S. mystax*). Thus, although the potential for competition between congeneric tamarin species is high for fruit resources, particularly at times of fruit scarcity (e.g., Terborgh, 1983; Garber, 1988b; Hardie, 1998), divergence in insect foraging may allow the two species to reduce the overall potential for inter-specific feeding competition and co-exist in mixed-species troops (e.g., Heymann, 1997; Heymann & Buchanan-Smith, submitted).

2.4.2 Vertical Segregation

The spatial structure of the tropical rain forest is three dimensionally complex in terms of the size and arrangement of potential supports for arboreal animals (Oates, 1987). However there does exist an order of organisation in the vertical plane resulting in vertical stratification of slightly different environments (Richards, 1952). The many species of animal within the rain forest differentiate themselves between these environments according to the location of their food resources, predation risk, and to intra- and inter-specific feeding competition. Such vertical segregation appears to be a major theme in the ecology of related sympatric animal species (e.g., Emmons, 1980; Richard, 1985) and sympatric tamarins are no exception. In all tamarin mixed-species troops studied thus far, *S. fuscicollis* occupies a lower stratum than its congeners (e.g., Yoneda, 1981, 1984a; Pook & Pook, 1982; Buchanan-Smith, 1990a, 1999; Hardie, 1998, for *S. fuscicollis* and *S. labiatus*; Garber, 1988b; Peres, 1992b, 1996, for *S. fuscicollis* and *S. mystax*; Terborgh, 1983; Buchanan-Smith, 1999, for *S. fuscicollis* and *S. imperator*). As mentioned earlier, this may have consequences for the detection of resources at different heights in the forest. Both species in the mixed-species troops increasing their foraging efficiency by capitalising upon resources located by their congeners in a different forest stratum (e.g., Peres, 1996). Moreover, given that tamarin species in mixed-species troops are known to respond to each other's alarm calls about potential predators (e.g., Buchanan-Smith, 1990a; Heymann, 1990b; Peres, 1993a), if the different species are more alert for predators at their particular height in the forest, then the anti-predatory behaviour of each species will be complementary. There are strong field data to support this. Peres (1993a) has shown that wild *S. fuscicollis* are more vigilant at lower levels of the forest, perform more downward scanning, and detect more terrestrial and scansorial threats than their congeners. In contrast, *S. mystax*, which are more vigilant at higher levels, perform more sideways and upward scans, and detect more aerial and arboreal threats. Given that the greatest predatory threat to tamarins is probably from raptors (e.g., Terborgh, 1983; Goldizen, 1987b; Heymann, 1990b), the vigilance behaviour of *S. mystax* may be particularly important for the survival of individuals of both species in the mixed-species troop. However, terrestrial and scansorial predatory mammals, such as small-sized felids and mustelids are likely to pose a threat to tamarins also (e.g., Emmons, 1987; Stafford & Ferreira, 1995; Buchanan-Smith & Hardie, 1997). Since the vigilance behaviour of *S. fuscicollis* is likely to be more effective in the detection of such threats, its importance should not be discounted.

Vertical segregation may also have consequences for the partitioning of shared resources between associating species and for ameliorating the intensity of inter-specific interactions (Heymann & Buchanan-Smith, submitted). This proposition will be examined in more detail in Chapter 8. Such benefits, accrued to associating species through vertical segregation, obviously do not apply to similarly-sized single-species troops.

2.4.3 Decreased Breeding Competition

While in many primate species, increasing troop size may increase the opportunities for troop members to breed, this does not appear to be the case for most members of tamarin troops. This is because, as described earlier, within tamarin troops there is rarely more than one reproductively active female (e.g., Yoneda, 1981, 1984a,b; Pook & Pook, 1982; Snowdon & Soini, 1988), with few recorded exceptions (Terborgh & Goldizen, 1985), although there may be more than one reproductively active male mating with this female (Terborgh & Goldizen, 1985; Heymann, 1996). In any case, the breeding female usually maintains exclusive mating by suppressing ovulation in subordinate conspecific females, probably through an olfactorily mediated mechanism (e.g., Epple & Katz, 1984, for *S. fuscicollis*). Consequently, reproductive output within the troop is limited, regardless of its size (see Section 1.2.3). Individuals in single-species troops may therefore have to trade-off the assumed increased survival chances of living in larger troops, against this increased breeding competition. It may even be that large single-species troop size is unattainable due to severe socio-sexual conflict as a result of this breeding constraint, resulting in troop sizes which are below the optimal troop size for maximum advantage through predator detection, feeding efficiency, or any other benefits of sociality. By forming mixed-species troops, however, participating individuals may gain all the advantages of larger troop size, but without the increased breeding competition similarly-sized single-species troops would face (Buchanan-Smith, 1989; Buchanan-Smith & Hardie, 1997; Peres, 1991). Such a proposition is extremely difficult to test given the difficulties of obtaining long-term data on the reproductive success of individuals in wild single- and mixed-species tamarin troops.

2.5 Associative Asymmetry in Tamarin Mixed-Species Troops

Probably no single evolutionary cause explains the general phenomenon of inter-specific association in primates, and the precise nature of what is exchanged is only slowly becoming explicit. In tamarins, the mutualistic interactions between associated species appear to connote a direct exchange of benefits at low cost (e.g., Terborgh, 1983; Norconk, 1986, 1990a; Hardie, 1995; Heymann & Buchanan-Smith, submitted) since both species actively maintain the association. Waser (1987) writes that

> *"where associations can be shown to involve behavioural attraction between species, positive effects must be strong; behavioural attraction is prima facie evidence that selection has favoured associating"* (p. 218).

However, the costs and benefits of association may differ for each species (e.g., Terborgh, 1983; Peres, 1992a,b, 1993a; Hardie, 1995, 1998) for different individuals, and between sites depending upon factors such as population density, resource availability, distribution and renewal rates (Garber, 1988b). In all tamarin mixed-species associations studied thus far, *S. fuscicollis* are subordinate to their larger congeners (e.g, Terborgh, 1983; Buchanan-Smith, 1990a; Heymann, 1990a; Peres, 1996). This may result in asymmetry in the costs of association through aggressive encounters and exclusion from feeding sites. Although inter-specific social interactions are infrequent, they are mostly agonistic (Yoneda, 1981; Buchanan-Smith, 1990a; Heymann, 1990b; Norconk, 1990b), usually occur in small feeding trees (Terborgh, 1983; Buchanan-Smith, 1989; Peres, 1993b), and often result in displacement of *S. fuscicollis* from the desired area (Terborgh 1983; Buchanan-Smith, 1990a; Heymann, 1990a; Hardie, 1998; Peres, 1996). For example, Peres (1996) has demonstrated that *S. fuscicollis* are often displaced from small, monopolisable undercanopy trees by *S. mystax*, even though they are the species to discover such resources most often.

Terborgh (1983) notes that, when foraging in mixed-species troops with *S. imperator*, *S. fuscicollis* tend to follow their congener in their progression through the forest. However, on the approach to the "best feeding sites", *S. fuscicollis* run ahead and may therefore offset the cost of exclusion by arriving and feeding at these sites before their congener (pre-emption), thereby obtaining more and higher quality food. However, the "best feeding sites" Terborgh refers to, are probably large, productive feeding trees that are likely to be non-monopolisable and allow both species to feed simultaneously anyway. In other associations, *S. fuscicollis* are again reported to follow their congeners (Buchanan-Smith, 1990a; Hardie, 1998; for *S. labiatus*; Peres, 1991; for *S. mystax*). In this respect, Buchanan-Smith and Hardie (1997) suggest that where resource patches are large, as was the case in mixed-species troops of *S. fuscicollis* and *S. labiatus* in Bolivia (Buchanan-Smith, 1991a) and *S. fuscicollis* and *S. mystax* in Peru (Peres, 1993b), *S. fuscicollis* need not arrive first to ensure they acquire sufficient food.

Asymmetry may also occur in the vigilance benefits accrued to the different species in mixed-species troops. Peres (1993a) found that, in a mixed-species troop of *S. fuscicollis* and *S. mystax*, *S. mystax* scanned proportionately more than its congener. This, combined with the fact that *S. mystax* had a larger troop size than its congener, meant that *S. fuscicollis* gained more anti-predatory benefit from the association than did *S. mystax*. *S. labiatus* has been found to look up significantly more than *S. fuscicollis* in both single and mixed-species troops in captivity (although their overall vigilance rates did not differ) (Buchanan-Smith & Hardie, 1997). In support of the proposal that *S. fuscicollis* takes advantage of the upward scanning of their congeners, *S. fuscicollis* performed less looking up in mixed-species troops than in single-species troops, whereas the rate of looking up for *S. labiatus* did not differ.

Further asymmetry may occur as a result of inequality in the effort invested in territorial defence. Peres (1992a) has shown that *S. mystax* invest more in territorial defence than do their congeners; have a higher frequency of (inter-specific) encounters, more physical contact, and receive more injuries than *S. fuscicollis*. In view of the greater investment by *S. mystax*, Peres states that *S. fuscicollis* may be "*enjoying a protective shadow against resource depletion*" (p. 243). In addition, although contributing less to territorial defence, *S. fuscicollis* appear to derive greater benefit, in the form of increased prey foraging efficiency, from exclusive use of the defended space because of their reliance upon highly depleteable insect prey which are found in higher numbers in the territory centre compared its periphery, and which suffer a greater impact from intra-specific competition than do the scattered, mobile insect prey of *S. mystax* (Peres, 1992a).

So tamarin mixed-species associations appear to connote a direct exchange of benefits at low cost, but the benefits and costs may be different or asymmetrical between species (summarised in Table 2.1). For example, although the cost of increased feeding competition may be greater to *S. fuscicollis* on account of their subordinancy to their congeners, they may accrue greater benefits through associating than do their congeners in the form of flushed insect prey and from the greater investment of their congeners in vigilance and territorial defence. However, regardless of any asymmetry in costs or benefits, Peres (1992b) writes that

Table 2.1: Proposed costs and benefits of association for *S. fuscicollis* and the members of the *S. mystax* group. Actual documented costs and benefits are cited in brackets.

	***S. mystax* group**	***S. fuscicollis***
COSTS		
(1) Increased feeding competition	(a) Loss of food through exploitative competition. (Terborgh, 1983, reports increased travel cost for *S. imperator* in mixed-troops with *S. fuscicollis*).	(a) Loss of food through exploitative competition.
		(b) *S. fuscicollis* suffer interference competition because they can be displaced from feeding sites by their dominant congeners. (e.g., Buchanan-Smith, 1990a; Hardie, 1998, for mixed-troops of *S. fuscicollis* and *S. labiatus*; Peres, 1996, for mixed-troops of *S. fuscicollis* and *S. mystax*).
(2) Maintenance costs	(a) Increased energetic expenditure and conspicuity due to increased calling, backtracking when separated and choosing sleeping sites close to one another.	(a) Increased energetic expenditure and conspicuity due to increased calling, backtracking when separated and choosing sleeping sites close to one another.
BENEFITS		
(1) Decreased predation risk	(a) Gain in overall troop vigilance. (Hardie & Buchanan-Smith, 1997, for mixed-troops of *S. fuscicollis* and *S. labiatus* in captivity).	(a) Gain in overall troop vigilance. (Hardie & Buchanan-Smith, 1997, for mixed-troops of *S. fuscicollis* and *S. labiatus* in captivity).
	(b) Reduction in individual vigilance level. (Hardie & Buchanan-Smith, 1997, for mixed-troops of *S. fuscicollis* and *S. labiatus* in captivity).	(b) Reduction in individual vigilance level. (Hardie & Buchanan-Smith, 1997, for mixed-troops of *S. fuscicollis* and *S. labiatus* in captivity).
	(c) Complementary vigilance benefits from the monitoring of terrestrial and scansorial threats by *S. fuscicollis*.	(c) Complementary vigilance benefits from the monitoring of aerial and arboreal threats by members of the *S. mystax* group.

	(Peres, 1993a, for mixed-troops of *S. fuscicollis* and *S. mystax*).	(Peres, 1993a, for mixed-troops of *S. fuscicollis* and *S. mystax*).
		(Peres, 1993a, also reports that *S. fuscicollis* may benefit more due to greater investment in vigilance by *S. mystax*).
	(d) Can parasatise knowledge from the reactions of *S. fuscicollis* to predators.	(d) Can parasatise knowledge from the reactions of *S. mystax* group to predators.
(2) Increased foraging efficiency	(a) Sharing or parasitism of knowledge about food.	(a) Sharing or parasitism of knowledge about food.
	(Hardie, 1995, reports transfer of knowledge about the presence of food in both captive *S. fuscicollis* and *S. labiatus*).	(Hardie, 1995, reports transfer of knowledge about the presence of food in both captive *S. fuscicollis* and *S. labiatus*).
	(b) Access to otherwise unavailable food (probably rare for members of the *S. mystax* group).	(b) Access to otherwise unavailable food.
		(Peres, 1992b, reports *S. mystax* flushing insect prey to *S. fuscicollis*).
	(c) Guiding to food resources.	(c) Guiding to food resources.
	(Peres, 1996, reports *S. fuscicollis* guides *S. mystax* to small, monopolisable food resources).	(Peres, 1996, reports *S. mystax* guides *S. fuscicollis* to large, non-monopolisable food resources).
	(d) More efficient use of resources: avoidance of previously used areas and regulation of return times.	(d) More efficient use of resources: avoidance of previously used areas and regulation of return times.
(3) Increased resource defence	(a) Increased ability to defend resources due to increase in troop size in mixed-species troops.	(a) Increased ability to defend resources due to increase in troop size in mixed-species troops.
	(Garber, 1988b, reports an increase in the number of *S. mystax* in a mixed-troop of *S. fuscicollis* and *S. mystax* increased its ability to defend resources).	(Peres, 1992a, reports that *S. fuscicollis* may benefit more due to greater investment in territorial defence by *S. mystax*).
(4) Decreased breeding competition	(a) Avoidance of increased breeding competition accrued in large single-species troops by forming mixed-species troops instead.	(a) Avoidance of increased breeding competition accrued in large single-species troops by forming mixed-species troops instead.

"mixed-species groups...should evolve and remain stable so long as the ensuing benefits are greater than the costs for each species independently, *given the ever-present alternative of monospecific life"* (p. 346).

In order to show conclusively that, for a given species, mixed-species troops are adaptive over alternatives such as single-species troops, it is necessary to show that individuals of that species ultimately experience greater survival and reproduction rates in mixed-species troops than in single-species troops. There is some evidence that *S. fuscicollis* may achieve significantly higher population densities in areas where it associates with a congener in comparison with sites at which it does not, and that this is particularly apparent for associations with *S. mystax* and *S. labiatus* (Norconk, 1990b). Drawing data from thirteen studies encompassing twenty localities, Norconk found the mean population densities of *S. fuscicollis* in association with *S. mystax* and *S. labiatus* to be 24.5 and 24.0 individuals per km^2 respectively, compared to 12.6 individuals per km^2 in areas where they do not associate. It is thus possible that, without excluding local differences in habitat quality, habitat disturbance, and the presence of primate or non-primate competitors that could limit the population growth of *S. fuscicollis* in the absence of a congener, the presence of a congener has a positive effect on the population densities of *S. fuscicollis*. Perhaps *S. fuscicollis* in mixed-species troops are less likely to be preyed upon than *S. fuscicollis* in monospecific troops. Further evidence for enhanced population growth comes indirectly from cropped populations (where individuals are trapped and removed). At one site in Peru, the ratio of *S. fuscicollis* to *S. mystax* was 1.3 individuals per km^2 before an extensive trapping program in which 186 *S. mystax* and 27 *S. fuscicollis* individuals were removed. Five years after the program, the ratio had decreased to 0.82 showing that *S. mystax* population densities post-program were higher than those preprogram, while *S. fuscicollis* densities showed a decline (Glander *et al.*, 1984). The fact that the population densities of *S. fuscicollis* declined after the loss of *S. mystax* again suggests that *S. fuscicollis* gain from associating. However, little is known regards normal fluctuations in population densities for tamarins, so intepretation of these results must remain tentative.

Just as the costs and benefits of association may differ for different species because of the different selective pressures subject upon them, they may also differ for different individuals according to their age, sex or social status. For example, due to their small size and limited experience, juveniles are expected to face higher risks of predation and be less efficient foragers than adults. The anti-predatory and foraging benefits accrued to individuals in mixed-species troops may thus be greater for juveniles than for adults. With regards to differences in the costs and benefits to different sexes in mixed-species troops, remember that, as described earlier, although there may be more than one breeding male in tamarin troops, there is generally only one breeding female and this dominant female suppresses reproduction in all other females. Individuals of both sexes in single-species troops may therefore have to trade-off the assumed increased survival chances of living in large troops against increased breeding competition. By forming mixed-species troops, however, participating individuals may gain all the advantages of larger troop size, but without the increased breeding competition similarly-sized single-species troops would face (e.g., Buchanan-Smith, 1989). Freedom from breeding competition may be particularly important for females given that polyandry is more common than polygyny in tamarins (Peres, 1991).

Sex differences in tamarins are not only functionally plausible but are a real and robust phenomenon. For example, Mayer *et al.* (1992) found adult female *S. labiatus* to be more persistent in searching for food than adult males when foraging in captivity. Similarly, Box (1997) has demonstrated that adult female *S. fuscicollis* and *S. labiatus* attempt unfamiliar foraging tasks (extraction of embedded food from perspex boxes) more frequently than adult males, spend longer periods attempting to obtain the food, and remove food from the boxes more often. Given that both sexes are physically able to complete the task, these results were considered as evidence for male deference to the breeding female during feeding in exchange for opportunities to breed with her. However, since non-breeding adult females also had priority of access to food, it is relevant to consider that the different sexes have different characteristic behavioural propensities or responsiveness in situations such as foraging, apart from the direct influence of reproductive status. In this regard, immature and non-breeding adult daughter tamarins have been observed to be especially responsive to elements in their physical environments (Price, 1992; McGrew & McLuckie, 1986, for *S. oedipus*), whereas, in contrast, males (including breeding males) have been reported to be less exploratory (at least initially). Male tamarins are more likely to be vigilant than females (Caine, 1987, for *S. labiatus*; Buchanan-Smith, in press, for *S. fuscicollis* and *S. labiatus*), and Goldizen (1989) reports that sentinel individuals in *S. fuscicollis* are typically adult males. This may mean that males benefit more from mixed-species troop formation than do females, since the reduction in individual vigilance and increased detection of predators accrued through the addition of extra males (and females) in mixed-species troops will have a greater impact on their vigilance behaviour than that of females. This may apply particularly to male *S. labiatus* and *S. mystax* in association since they are reported to shoulder more of the vigilance burden (invest more in vigilance behaviour) than *S. fuscicollis*. Even within the same sex not all individuals are equal (although tamarin societies appear to be more egalitarian than many other primate societies: Caine, 1993). For example, the dominant (breeding) female may accrue greater benefits compared to subordinate females (and males) from increased prey capture rates in mixed-species troops. Since animal prey (mostly insects) represents the highest quality dietary component of wild tamarins, flushed insects may provide a special incentive for breeding females, heavily energetically-stressed by the large demands of pregnancy and lactation in tamarins, to associate. Heavily pregnant females, less able to negotiate the substrates of the forest, may also be more susceptible to predation than other females (and possibly males), and thus may also benefit more from the anti-predatory advantages of mixed-species troops.

All of the above factors are also likely to have a bearing on the probability and dynamics of social learning within mixed-species troops. Thus, apart from exploring functional hypotheses for the proximate advantages to individuals accrued through association, experiments on social learning in captivity can also be used to ask questions which relate specifically to the influence of the social properties of demonstrators (e.g. species, age, sex, social status) upon the behaviour of observers and vice versa. However, although individual animals' preferences, choices and 'personalities', and other individuals' responses to them, is an important topic (see Box, 1991; Clark, 1991), it is an exceedingly difficult one to study, precisely because of sample-size limitations. Nevertheless, in this thesis, I examined sex and age effects, in addition to species effects, in all of the experiments for which there was a sufficiently large sample size.

2.6 Optimal Troop Size in Tamarin Mixed-Species Troops

It has been hypothesised that limits to the size of animal groups are imposed by the ecological conditions their members experience, that is, the amount of food available to them (e.g., Clutton-Brock & Harvey, 1977a; Waser, 1977; Wrangham, 1980, 1983; Clark & Mangel, 1986; Elgar, 1989), the level of predation they encounter (e.g., Hamilton, 1971; Alexander, 1974; van Schaik & van Hoof, 1983; Hill & Lee, 1998), and the social system they adopt (e.g., Wrangham, 1980; van Schaik & van Hoof, 1983). Debate currently surrounds the relative strength of these selective pressures for primate troops. Some authors advocate predation as the largest single selective force acting to promote sociality (Crook, 1972; Rowell, 1979; van Schaik & van Hoof, 1983; Stacey, 1986; Caine, 1993). Others suggest inter-troop feeding competition accounts for the evolution of sociality, as large troops may be better at procuring and/or defending resources (Clutton-Brock & Harvey, 1977a; Wrangham, 1980, 1983, 1987; Wrangham *et al.*, 1993). Individual studies for primates have, in fact, given support to both theories and indeed it is highly probable that selection acts multi-directionally. Whatever the outcome of the polarising debate as to which selective pressure is the most important, there is a growing consensus that primate troops are affected by both predation avoidance and feeding competition (van Schaik, 1983; Dunbar, 1988; Terborgh & Janson, 1986; Terborgh, 1990; Janson & Goldsmith, 1995).

How do these selective pressures affect troop size in tamarin mixed-species troops? Tamarins are considered especially vulnerable to predation relative to other larger-bodied primates (Cheney & Wrangham, 1987; Terborgh, 1990; Caine, 1993), yet predation was initially discounted as the driving force in the formation of tamarin mixed-species associations (Terborgh, 1983). Rather, other ecological factors, such as feeding competition, were considered more important (Terborgh, 1983; Garber, 1988b). In support of this proposition Terborgh (1983) argued that, in mixed-species troops, *S. fuscicollis* and *S. imperator* do not act in a manner that optimises predator avoidance because they spend a considerable amount of their time out of visual contact with each other (around 20 - 50 m from each other, whereas the approximate limit of visual contact at his study site was 10 - 20 m). Moreover, the preponderance of attacks when the tamarins were in tall trees, coupled with frequent sequential feeding, led Terborgh to conclude that the species do not behave in such a way as to maximise their ability to reciprocate in predator warnings. This conclusion seems unfounded, however, given that, for tamarins, predator warnings are by way of alarm vocalisations and therefore do not necessitate visual contact. In fact, it appears that, by reacting to the alarm calls of their congeners, associating species can enhance their ability to avoid predation, compared to that of single-species troops (Peres, 1993a; Hardie & Buchanan-Smith, 1997).

In a more recent paper, Terborgh (1990) takes a more balanced view. Mixed-species tamarin associations are considered as adaptations for achieving an optimal balance between predator protection and feeding efficiency. In making some comparisons between the 'closed-habitat' associations of Amazonian bird species and those of Amazonian primates, he suggests that *"group limiting constraints of feeding competition interact with optimal predator avoidance to strike compromises at variable, but restricted group sizes"* (p. 94).

Many of the proposed benefits of group living tend to increase with group size (e.g., increased predator detection and avoidance). Yet sizes of wild tamarin troops appear to be constrained within quite narrow limits. Field studies consistently report intra-specific mean troop sizes of between five and seven individuals, and none has returned a mean troop size of more than seven. It is possible, therefore, that increases in intra-specific troop size in tamarins may only be advantageous up to a certain size, and that above this theoretical point, increased feeding competition sets an upper limit to troop size. Terborgh and Janson (1986) devised a model that predicts that, for any primate species, given the spatio-temporal dispersion of its major food resources, there exists an optimum troop size. This is the troop size which maximises the differential between the benefits of sociality and the costs. In the model, where feeding conditions mitigate against aggregation (i.e., whenever food resources are spatially restricted and/or slowly ripening), intra-specific competition for access to feeding sites imposes strong constraints on troop size. Under such conditions, small troops will be the rule, and protection from predators will be achieved through some means other than safety in numbers, such as crypsis. A compromise is struck that maximises individual lifetime reproductive success without maximising either security from predators nor individual feeding success. The authors suggests that this is the case for mixed-species troops of Amazonian primates, and Terborgh (1990) suggests that, in view of their closed habitats, such troops should be small, of fairly consistent size, and composed of few to many equally represented species, that may be cryptic but not convergent in their appearances, and whose maximal predatory advantage is through alarm signalling.

While acknowledging that ecological thresholds such as intra-troop feeding competition clearly limits the size of social groups in animals, Peres (1991) proposes that maximum intra-specific troop size in tamarins is more likely to be set by intra-specific breeding competition. As mentioned earlier, with few exceptions most tamarin troops have only a single, dominant breeding female (Moynihan, 1976; Garber, 1980, Garber *et al.*, 1984; Neyman, 1980; Terborgh, 1983; Terborgh & Goldizen, 1985; Buchanan-Smith, 1989). Thus the availability of breeding females in any given troop is limited. With regards to the number of breeding males per troop, although monogamy appears to be the most common mating system for tamarins, in many troops more than one male is observed to mate with the breeding female (polyandry). However, in these cases, paternity often cannot be ascribed, nor can it be easily inferred in a social system in which all males may contribute to rearing the offspring (e.g., Terborgh & Goldizen, 1985; Goldizen, 1989, 1990). The position regards the number of breeding males in tamarin troops is thus less clear than that of females. Whatever the case, a large troop of tamarins, containing many adults, will have at least sexually redundant females, and possibly sexually redundant males as well. This may make large monospecific troops a reproductive liability for some of their members and consequently they may be selected against (in favour of maximal troop sizes below the optimal for predator detection, avoidance, and other benefits of sociality). However, an increased number of individuals can breed, if a large number of small troops are formed, as opposed to a small number of large troops. In support of this theory, Peres (1991) points out that the intra-specific troop size of tamarins that live monospecifically is virtually identical to that of those living in mixed-species troops. He argues that breeding constraints have thus forced a maximum intra-specific troop size for all tamarin troops.

In summary, mixed-species tamarin associations may be adaptations for achieving the optimal troop size that maximises the differential between the benefits of sociality (e.g., increased predator avoidance) and the costs, namely intra-specific feeding and breeding competition.

2.7 Aims of the Thesis

For the most part, and especially in primates, hypotheses regarding the function of polyspecific associations have not been rigorously tested and support is often anecdotal or surmised. The broad aim of this thesis is to explore the foraging behaviour of single- and mixed-species troops of *S. f. weddelli* and *S. l. labiatus* in order to further understanding of the function of tamarin mixed-species troops in general and how social learning may play an adaptive role within them. The thesis also seeks to evaluate the biological and behavioural differences between the species that permit their association.

To evaluate the benefits (and costs) of association for members of a given species, a comparison of animals in and out of association is needed. Waser (1987) writes that such comparisons

> ***"come as close as is possible to controlling for habitat differences; when the same animals in the same place change their behaviour while associating with another species, the changes are convincingly related to the other species' presence"*** (p. 218).

Only three primatological studies have compared animals in and out of association (Gautier-Hion *et al.*, 1983; Cords, 1987, for guenons; Terborgh, 1983, for tamarins). The problems with utilising this approach for tamarin mixed-species associations are practical ones. For example, it is extremely difficult to make tests of functional hypotheses in the field because sympatric tamarin species are rarely found out of association. Terborgh (1983) writes

> ***"the crux of the problem lies in the contrast between what we actually observe and what we cannot observe - how the species would behave if there were no association and if they operated entirely independently of one another in overlapping territories"*** (p. 184).

Terborgh was lucky in that, in his study, one *S. fuscicollis* troop associated alternately with two mutually hostile *S. imperator* troops. This provided the opportunity to examine the behaviour of *S. imperator* in and out of association. In the captive environment, it is possible to test species singly and in mixed-species troops, whilst manipulating relevant variables experimentally under controlled conditions. To this end, the majority of the data presented in this thesis were collected at Belfast Zoological Gardens which provides a large sample size of monkeys in facilities off-exhibit to the public and on a par with many behavioural laboratories. An evaluation of the utility of testing the functional hypotheses proposed for wild tamarin mixed-species troops in captivity follows later in Chapter 4. Much of the captive data presented comes from experiments investigating social learning of foraging information within and between species in mixed-species troops. Social learning is implicated in the framework of many of the foraging benefit hypotheses proposed for tamarin mixed-species associations. However, although universally proposed, there is, as yet, little empirical evidence for sharing of knowledge in tamarin mixed-species troops (see Hardie, 1995; Peres, 1996; for notable exceptions). The following chapter examines the role of learning in foraging and details how social learning (i.e., learning from others or having one's learning influenced by others) can be a particularly adaptive way of acquiring foraging information and may play an important adaptive role in tamarin mixed-species troops.

Chapter 3

Foraging and Learning

"While learning theorists have forgotten that learning is an adaptation, behavioural ecologists generally have ignored the role of learning in the development of adaptation."

[Kamil & Yoerg, 1982: p. 325]

3.1 Introduction: An Integrated Psychological and Behavioural Ecological Perspective

Learning is clearly important in the study of foraging behaviour. For example, wherever the spatial and temporal distribution of food in the environment is non-random, mature animals can learn about the distribution, and thereby deal with it more efficiently. Naïve infant animals, maturing in a demanding environment, must learn a nutritionally adequate diet and to avoid potentially harmful food stuffs. However, to the extent that a species' success may also depend upon the ability to exploit new resources, it is important that all age classes sample and learn the characteristics of novel palatable foods and how they are to be to processed.

Investigations of animal learning have traditionally been the domain of psychologists. However, such psychological investigations of animal learning have emphasised mechanistic explanations whereas ecological and ethological investigations have tended to emphasise functional explanations. Complete understanding of learning phenomena requires both kinds of analysis, however, and the recent emergence of similar views of animals as decision makers in both psychology and behavioural ecology offers a unique opportunity for the development of interdisciplinary research and theory (Kamil, 1984). Foraging theorists can benefit from a knowledge of existing theories of psychological learning to help predict how animals track changes in their environment; and from the adoption of techniques, particularly from operant conditioning, to apply to foraging problems (e.g., Lea, 1979, 1981; Staddon, 1980; Olton *et al.*, 1981; Kamil & Yoerg, 1982). Conversely, a sizeable and rapidly growing literature in behavioural ecology has many implications for animal learning and cognition (e.g., Gill & Wolf, 1977; Kamil, 1978; Heinrich, 1979).

Kamil and Yoerg (1982) postulate that two factors in the ecological study of foraging, one methodological and one theoretical, have resulted in the recent interest in learning on the part of ecologists. The first factor is a dramatic increase in the number of field studies of foraging in which identifiable individuals are studied over extended periods of time. The data from many of these studies implicate learning and memory as important mechanisms in natural foraging situations. The increase in such studies is largely a consequence of the second factor; the development of *optimal foraging theory* (OFT) which conceptualises the forager as a decision maker using information about its environment to solve the problems it faces in its foraging. In many cases, this information must be acquired through learning, either independently of others (asocial learning) or as a result of interaction with others (social learning). Both OFT and social learning are central to this thesis. Little direct laboratory investigation of information acquisition through social interaction has been undertaken by ecologically-orientated researchers. The present study sets out to do just that and explores whether facilitation of social learning of foraging information is an advantage of mixed-species troop formation in tamarins. The adaptivity of social learning in general is discussed later in this chapter, along with a justification for expecting it to operate in tamarin troops. First, though, is a brief description of OFT. In exploring tamarin foraging behaviour, I make frequent direct or indirect references to OFT, particularly in Chapters 9 and 10. I therefore feel it necessary to describe exactly what it is and acknowledge its criticisms, particularly with reference to its application to primates. I do not wish to attempt a critical review of OFT, and for such a review, I refer the reader to Pyke (1984).

3.2 Optimal Foraging Theory

A major impetus towards the study of learning by ecologists has been provided by the development of OFT. At its simplest, OFT is a logical structure embodying a series of assumptions that generates, by deduction, falsifiable hypotheses about decision making during foraging (Post, 1984). Use of this structure enables the proponents of OFT to predict the behaviour of animals *while they are foraging.*

The basic logic of the OFT approach is quite simple. Suppose that animals vary in their foraging efficiency and that this variation has some heritable component. Then natural selection should favour those animals within a population that forage most efficiently. Given sufficient selection pressure and sufficient time within a relatively stable environment, selection should produce highly efficient foragers. In the limit, it should produce optimal foragers, animals who forage as efficiently as possible. OFT is thus based upon the assumption that through natural selection, animals have evolved so as to maximise their biological fitness.

The aim of OFT is to make an informed hypothesis about the nature of this 'efficiency' and the constraints that limit it. The basic approach is to build this hypothesis into a mathematical or graphical model of a specific problem that an animal regularly faces in nature, specifying a currency (i.e., what is to be optimised), and selecting the cost-benefit functions that, ideally, reflect real constraints on the forager. The model is then solved for its optimal solution (Schoener, 1971). The solution is then taken as a prediction and the hypothesis can be examined by testing the prediction (or in some cases, the assumptions of the model) against real data. Thus, OFT seeks to not to test the proposition that animals are (or are not) optimal, but only that one particular hypothesis, for example maximising net rate of energy intake subject to specified constraints, describes their foraging behaviour. That is, it seeks to test what competing demands and constraints they face and what means they employ to meet them.

Since its emergence as an exciting development in the 1970's, OFT has attracted much criticism, particularly on theoretical grounds. Debate generally centres around whether or not OFT is tautological and whether or not it is possible to test hypotheses about adaptation (e.g., Maynard Smith, 1978; Brady, 1979; Gould & Lewontin, 1979). For example, Gould and Lewontin (1979) contend that what is actually being tested in optimization studies is not what problems animals are facing in their foraging and how they are solving them optimally, but simply the researcher's ability to generate plausible conditions responsible for the occurrence of an observed trait or behaviour. In their opinion, OFT is adaptive story-telling or "*imaginative reconstruction*". However, in defence of OFT, Kamil and Yoerg (1982) state that, *"in a sense, all hypothesis and model formation is a kind of educated invention [though some inventions are more educated than others]"* (p. 344). The real issue is whether OFT is an appropriate and useful abstraction.

With regards to the application of OFT to primate foraging behaviour, there are a number of problems. For example, primates are remarkably versatile and opportunistic in their foraging behaviour, engaging in many kinds of search and capture activities (Terborgh, 1983). As such, they tend to exhibit more complex foraging strategies than non-primates (Garber, 1987; Grether *et al.*, 1992). Garber (1987) suggests that this is a function both of their environmental (habitat) complexity and their ability to learn complex environmental relationships which allow them to remember and evaluate disparate types of social and environmental information. Such complex foraging strategies may not be easily modelled by OFT. Moreover, primates typically inhabit tropical rain forests which are characterised by high tree species diversity and low species density (e.g., Chivers, 1977; Hubbell, 1979; Estrada, 1984; Robinson, 1986; Milton, 1988), and many tropical tree species exhibit a clumped distribution and are relatively predictable in their fruiting schedules. The rates at which primates encounter different food resources are thus rarely random and constant, as specified in most optimal foraging theories. Instead, they are often non-random as primates make use of complex foraging strategies relying upon previous experience and a knowledge of the location of appropriate feeding sites to increase their foraging efficiency (e.g., goal directed foraging: Hladik, 1977; Menzel, 1978; Milton, 1981; Terborgh, 1983; Robinson, 1986; Garber, 1987). Furthermore, in order to encounter a sufficient number of suitable food resources, primates must typically exhibit highly variable dietary patterns. That is, they do not forage according to a monotonous or narrow diet, so that in fulfilling their nutrient requirements, they consume many different types of food item. This violates another assumption of many optimal foraging theories. Instead, eclecticism is the rule for primate diets, with the great majority of primate species eating a combination of fruit, leaves and animal material to achieve a balanced diet (e.g., Harding, 1981; Harvey & Clutton-Brock, 1981; Bourlière, 1985; Richard, 1985). Moreover, since these different food types can exhibit seasonal and intra-specific differences in nutrient content, dietary sampling is a critical feature of primate foraging patterns. As a result, they tend to exhibit partial preferences for these resources (i.e., resource patches are not totally depleted after a feeding bout but are exploited within a bout until satiation occurs on that food type), and these preferences may alter depending on seasonal variation in nutrient content. Given the violation of many of the assumptions of early OFT models (e.g., sequential encounter of food types, at a constant rate, independent of past experience; constant dietary choices without sampling or partial preferences), Garber (1987) writes that

> *"In their present state, optimal foraging models are of only limited use in understanding and predicting primate behaviour. This results from the fact that many of the assumptions of optimal foraging are inappropriate for....animals that rely heavily on cognition and past experience in foraging decisions."* (p. 356).

The application of OFT to mixed-species troops may be further problematic. For individuals deriving fitness benefits from grouping, it is necessary that they remain within the group in order to accrue these. This is certainly the case for individuals in primate troops where troop cohesion and strong mutual interdependence of troop members has fundamental survival value (Cambefort, 1981). However, the need to follow one's troop-mates or troop-leaders, or simply to keep one's troop-mates under constant surveillance, likely constrains the movement of individual animals about their home range quite considerably. Social constraints of this kind are not easily incorporated into OFT models. Modelling the foraging behaviour of individuals in mixed-species troops is particularly problematic in this regard, given that, in order to keep the association intact, at least one species may have to deviate from its optimal foraging pattern in order to follow the other species with which it may not even have an identical diet.

Despite these problems, I believe that there are instances in which OFT is of use to the primatologist in evaluating primate feeding and foraging patterns. Experiments in the latter part of this thesis examine the response of foraging tamarins to variability in their environment and how association affects this response. Looking at foraging adaptations and the adaptive value of association from the perspective of the *problems* faced by a primate in finding and acquiring food necessitates some optimal foraging theorisation. A focus on problems and their solutions is basic in all optimal foraging studies (e.g., Pyke *et al.*, 1977) and as such OFT can be used as an explanatory framework. Its potential utility as such a tool is profound (Post, 1984). Recent developments in OFT, including an increasing realisation of the potential importance of stochasticity in foraging models (e.g., Oaten, 1977; Pyke, 1978; Maynard-Smith, 1978; Caraco *et al.*, 1980; Stephens & Charnov, 1982) and the alteration of a number of assumptions present in the original foraging models (Elner & Hughes, 1978; Hughes, 1979), have freed it from many of its initial constraints and widened its applicability and realism. (Thus, the initial reluctance to apply OFT to foraging in primates, precisely because of the difficulty in doing so, can now be realistically overcome, and must be, if the study of primate foraging behaviour is to advance at the rate at which the study of foraging in other taxonomic orders has).

OFT originated with the assumption that foraging behaviour is perfectly adapted. But the most important aspect of OFT may prove to be that it has drawn attention to the critical dimensions of the distribution of food in nature and the sensitivity of foraging animals to those distributions. For many animals this sensitivity is a product of learning. The value of OFT may lie not so much in its theoretical foundations as in its heuristic function. If it provides a valuable tool in elucidating the specific nature of the relationship between animal and environment, then its use is justified, as it is here.

3.3 The Adaptivity of Social Learning

During their lifetimes, individual animals can acquire behaviour patterns in one of two ways: by asocial learning or by social learning. Asocial (independent) learning refers to behaviour acquired by an animal as a result of its *own* experience of the rewards and punishments contingent upon engaging in various acts (e.g., trial and error learning, operant conditioning). Social learning refers to those instances in which the acquisition of behaviour is influenced by observation of, or interaction with, another animal or its products (Heyes, 1994). It is important to note here that, in all cases of social learning, it is ultimately individuals who learn. Social learning might thus best be described as socially biased individual learning (Galef, 1995). Both types of learning are forms of phenotypic plasticity enabling animals to acquire behaviour that is adaptive in their local habitat (Boyd & Richerson, 1988) and may play supplementary or complementary roles in behavioural development (depending upon the different patterns of costs and benefits that make one or the other superior in any given environment) (Galef, 1995).

The survival value of the ability to acquire patterns of behaviour as a result of interaction with others, as well as from direct transactions with non-social aspects of the environment, is relatively straightforward. According to laboratory learning paradigms, the trial and error processes necessary for asocial acquisition of adaptive patterns of behaviour are often both energy-consuming and error-filled undertakings for the acquirer (Galef, 1976). Social learning provides an alternative, optimal route to asocial learning by allowing animals to learn about their environments more rapidly, uniformly and effectively, without making costly mistakes or wasting time on exploration (Galef, 1995). It is widely accepted that the ability to learn from others is an important adaptation that allows many animals to acquire information important for survival (adaptive behaviour) at low cost (e.g., Bateson, 1988; Plotkin, 1988).

An ability to learn from others, or to have one's learning influenced in an adaptive direction, may be important in two main contexts: (a) as naïve, vulnerable young, and (b) as adults in changing environments.

(a) The rapid acquisition of behavioural patterns necessary for survival within a particular habitat must be a particularly acute challenge for young animals, newly recruited to a population. Such individuals face impressive odds in having to learn not only how to find, identify and process the dietary constituents necessary for their subsistence, but also how to escape or avoid potential predators, and how to behave appropriately with conspecific individuals. It would be clearly advantageous to young if they could incorporate into their own behavioural repertoires the learned adaptive, rewarding behaviour of their more experienced parents, or other experienced adult conspecifics, through some process less cumbersome than *de novo* trial and error learning. Social learning is such a process and reduces the time, energy and risk associated with acquiring the behaviours necessary for survival during a time when individuals are likely to be most vulnerable to environmental stress and when errors in response thus have particularly serious consequences (Galef, 1996a).

(b) Adult organisms living in unstable environments could also benefit considerably from the social acquisition of conspecific patterns of behaviour. In the absence of such acquisition, each individual would have to discover for itself the existence or novel distribution of important elements in the environment following environmental change and learn for itself how best to deal with them. Social learning, however, can help adults monitor, track and deal with, the ebb and flow of resources in changing environments more quickly and efficiently than they could do so alone (Galef, 1993, 1996b). This is extremely important. Conversely, it is also important in nature that behavioural innovations be 'reversed' if novel ecological conditions make that more advantageous, because considerable costs may be incurred under conditions in which social traditions are not advantageous in particular ecological (and social) circumstances (Box, 1984). In general then, social learning allows populations to maintain established adaptive patterns of behaviour, but also to incorporate novel ones into their repertoires safely and rapidly (Mainardi, 1970, 1973, cited in Galef, 1976).

This thesis is concerned primarily with social learning of foraging information. Social learning of such information can proceed along routes of varying complexity (Galef, 1988; Whiten & Ham, 1992; Heyes, 1994). For example, in simple cases, the feeding behaviour of a conspecific may alter the physical environment in a way that increases the probability that its fellows will acquire that same behaviour. In more complex instances, a naïve animal might learn a complex feeding behaviour by observing and then imitating an accomplished knowledgeable conspecific. In yet others, individuals might actively teach conspecifics. However, with the possible exception of the apes, there is little convincing evidence of imitation, or teaching in non-human primates (i.e., teaching in the sense that the teacher *intends* that another acquire a feeding skill or piece of knowledge and actively adjusts its behaviour contingent upon its *attribution* of that other's progress in skill or knowledge) (Galef, 1990; Visalberghi & Fragaszy, 1996; Tomasello & Call, 1997). In fact, in all but a few instances, transmission of behaviour in non-human primates appears to result, in the large part, from the introduction by one individual of another into a stimulus situation to which the second individual is predisposed either as a result of previous experience or of instinctive tendencies, to respond in such a way as to acquire the behaviour of the first (Galef, 1976, 1988; Whiten & Ham, 1992; Fragaszy & Visalberghi, 1996). (In this respect, the tendency for young animals to remain in close proximity to conspecific adults may result in their acquiring adult feeding habits or responses to potentially dangerous stimuli). More correctly, the particular response acquired is likely to depend upon a combination of the second individual's experience of, and reaction to, the stimulus events to which it has been introduced by the first individual, and to the reaction of the first individual themselves to those same stimulus events.

Although there is little doubt that social learning can lead to the generation and transmission of adaptive behaviour (Galef, 1995), it is less clear whether social learning processes can lead to the transmission of maladaptive behaviour also (i.e., behaviour that reduces the fitness of the learner relative to an alternative behavioural pattern, and that leads to sub-optimal behavioural traditions) (Laland & Williams, 1998). Theoretical models exploring the adaptive value of social learning have led to the conclusion that it can (e.g., Boyd & Richerson, 1985, 1988; Rogers, 1988; Dawkins, 1989; Laland *et al.*, 1996). The proposition is that, in extreme temporally (or geographically) variable environments, environmental information transmitted between individuals is likely to become outdated or locally inappropriate very quickly. Thus, in such environments, animals relying on social learning (over asocial learning) will be at a disadvantage in that socially transmitted behaviours/traditions will constantly trail behind the environmental state if there is not enough time (for individuals) to adjust to the optimal behavioural pattern before a new one becomes best. Under such circumstances, reliance upon immediate, independent personal experience (asocial learning) is a more reliable strategy (Laland & Williams, 1998). Such claims that social learning is unlikely to be adaptive in changing environments have caused much controversy amongst learning theorists. One of their foremost critics is Galef (1995, 1996c) who suggests that maladaptive behaviour is unlikely to be transmitted or expressed by the learner because both the demonstrator of the behaviour pattern and the learner can rapidly adjust their behaviour to local conditions. The crux of the debate thus appears to relate to the speed with which appropriate behavioural responses can be made to novel/changing environmental circumstances. However, Galef (1976, 1995) points out that, since the maintenance of any behavioural pattern in the repertoire of an individual depends upon the reinforcement contingent upon engaging in that behaviour, no learned behaviour, no matter how it is acquired (socially or asocially), will be long maintained in an individual's repertoire unless it is at least as likely to produce rewards as are the available alternatives. Therefore, once introduced into a population, stable, socially learned behavioural patterns that do not garner disproportionate rewards from the environment (i.e., socially learned behaviour patterns that are not adaptive), will be selected against and should be rare and ephemeral, rather than common and persistent as the models by Boyd and Richerson (1988), Rogers (1988), and Dawkins (1989) allow. Whatever the outcome of this debate, there is little doubt that animal social learning is typically adaptive and that, in environments that do not change too rapidly, behavioural traditions will eventually converge upon the optimal behaviour for that environment. Such a behaviour will remain stable in the face of consistent positive reinforcement favouring the optimal solution.

3.4 Living in a Co-operative, Cohesive Troop as a Precursor of Social Learning

Living in a group is expected to vastly increase the scope of social transmission of behaviour because it facilitates close contact with a wide range of individuals. There are more animals to learn from, have one's learning influenced by, and to respond to more often (Bertram, 1978; but see Lefebvre *et al.*, 1996; Lefebvre & Giraldeau, 1996). However, although sociality provides occasion for social learning, it does not necessarily produce it (Fragaszy & Visalberghi, 1996; Lefebvre *et al.*, 1996). Most primates live as members of social troops throughout their lives, many with permanent social relationships, and are thus provided with numerous opportunities for modifying their behaviour through social learning. Given that primates have perhaps the greatest learning capacity of all mammals (Cambefort, 1981), it is entirely plausible that members of primate troops can and do learn much from observation of, and interaction with, their fellows.

In addition, living in a group frequently means that offspring remain in close contact with their parents for a long period. During this time, a great deal of learning no doubt takes place. Having more companions to observe and for longer presumably increases enormously the amount which can be learnt socially instead of by individual trial and error. Moreover, compared to other young mammals, primates experience a relatively extended period of infancy and juvelescence (e.g., McKenna, 1981; Box, 1984). Primate neotonates are born much less precocious than other K-selected animals (Pianka, 1988). They are relatively helpless at birth, particularly with regards locomotor behaviour, and must ordinarily be transported by the mother or other infant care-givers for a number of weeks, or more usually months, after birth. Moreover, maturation in monkeys, apes and humans is exceedingly slow both socially and biologically. It is ordinarily assumed that this delayed social and biological maturity (neoteny) is due, in part, to the learning demands faced by them. A long period of time is thus spent in intimate association with a parent, parents, or team of care-givers, who, by virtue of their reproductive success, demonstrate the adaptive behaviours necessary for survival (for example, the nutritional adequacy of the food they have been eating). Cambefort (1981) suggests that almost all the daily elements of adult primate social life are learnt and that, amongst them, feeding takes a particular place. He proposes that the whole feeding culture of the troop, not only knowing the palatable species of plants and animals, but also their location, techniques of acquisition, processing and consuming, has to be learnt during infancy and juvelescence, at first by observing the mother (or other care-givers or carriers) and later by watching the other troop members. Hall (1963) goes as far as to say, because of the natural affectional context in which the young of primates develop, a tendency to learn by observing others is characteristic of all young monkeys and apes. Moreover, young primates are highly exploratory and inquisitive and furthermore tend to explore selectively what others explore (Hall, 1963; Goodall, 1973; Prescott; pers. obs.).

Not only are primate species predominantly social but, in addition, many primate societies are habitually stable and long-lasting, consisting of related, mutually dependent individuals (see Crook, 1970; Clutton-Brock & Harvey, 1976). A result of this stability of troop composition, is that troop members can recognise one another individually and can learn a great deal about one another, both of which allow the evolution of complex social relationships, such as co-operative behaviour, through the operation of reciprocal altruism and, in related troops, kin selection (e.g., Hamilton, 1964). This co-operation may take the form of food-sharing, shared vigilance, or helping to rear the offspring of relatives: all of which may raise the inclusive fitness of the related co-operator (Hamilton, 1964). Of course, the extent to which individuals co-operate depends upon the costs and benefits to them of alternative strategies, and the degree of relatedness of the interactants. If individuals are closely related, then the selective pressure to compete is reduced, whilst that to co-operate is increased, through kin selection. Co-operative behaviour leads to increased proximity and an increased frequency of interaction, both of which are likely to favour social learning. Moreover, if individuals are close relatives, they are likely to be favourably disposed towards learners, which may help learners learn more and faster (Bertram, 1978).

Tamarin societies generally consist of stable, close-knit, extended family troops and are characterised by high levels of co-operation, tolerance and adaptability (Caine, 1993). When travelling and foraging, troop members move in a cohesive manner (e.g., Yoneda, 1984a; Goldizen, 1987b, for *S. fuscicollis*; Garber 1988b, for *S. mystax*; Buchanan-Smith, 1989, for *S. labiatus*) and when palatable food is found, even if only in small amounts, food calls are given which are thought to recruit troop mates to the vicinity of the caller (Addington 1992; Caine *et al.*, 1995, for *S. labiatus*). Tamarins also produce contact calls (Moody & Menzel, 1976, for *S. fuscicollis*; Caine & Stevens, 1990, for *S. labiatus*) which allow individuals to keep track of their troop mates, thereby maintaining cohesiveness within the troop, enabling movement in a co-ordinated manner and permitting co-operative ventures such as infant care and vigilance (Caine & Stevens, 1990). Infant tamarins require intensive carrying during the first 10 - 12 weeks of life and both parents and non-parent helpers (often older offspring) help in the carrying (Goldizen, 1987a). In *S. labiatus*, troop members actually compete to carry infants (Pryce, 1988). Helpers also share food with the infants (which can continue until 7 to 9 months of age), play with, clean and groom infants, and defend them against predators (Feistner, 1985; Goldizen & Terborgh, 1986; Goldizen, 1987a; Savage *et al.*, 1989; Feistner & Price, 1990; Heymann, 1990c; Price 1990a; Peres, 1991). With regards vigilance, in both *S. fuscicollis* and *S. labiatus*, individuals take turns acting as sentinels for one another (Goldizen, 1987b; Zullo & Caine, 1988). Furthermore, intra-troop aggression is rare (Goldizen, 1989; Buchanan-Smith, 1990a, for *S. fuscicollis*; Coates & Poole, 1983 for *S. labiatus*) and, in comparison with squirrel monkeys (*Saimiri*), tamarins are reported to be tolerant of each other's presence at a newly discovered food source (Mayer *et al.,* 1992 for *S. labiatus*). It has been argued that this general and uniform high level of co-operative behaviour in tamarins is best understood as a response to high predation risk and the consequent dependence upon troop mates (Caine, 1993). Whatever the proximate and ultimate factors for its evolution, however, its presence is likely to be connected to the high degree of relatedness between troop members. Again, as stated earlier, co-operative behaviour and high degrees of relatedness are likely to favour social learning.

Not only do tamarins co-operate intra-specifically, but also inter-specifically. As described in Chapter 1, *S. fuscicollis* forms stable and permanent mixed-species troops with three other species with which it is sympatric. These are *S. mystax*, *S. labiatus* and *S. imperator*. The most stable association is that between *S. fuscicollis* and *S. mystax*, that between *S. fuscicollis* and *S. labiatus* is intermediate, and *S. fuscicollis* and *S. imperator* associate the least (Heymann, 1997; Buchanan-Smith, 1999). Associating species defend a shared home range in parallel against neighbouring mixed-species troops (each species directing their aggression towards their conspecific rival) and co-ordinate their activity and movement to a remarkable degree, moving about the home range as a single cohesive unit (typically within 20 - 50 m of each other). Both species use vocal communication to maintain this intra-troop cohesion and are known respond to each other's alarm calls. Participating species also exhibit high overlap in the percentage of plant species eaten. When feeding together at monopolisable food resources, however, the smaller *S. fuscicollis* are often either supplanted by their larger, dominant congeners or are forced to wait until their congeners have finished eating before they can gain access to the resource.

Tamarins spend a great deal of their time foraging for food. *S. fuscicollis*, for example, are reported to spend around 60 % of their daily activity period foraging for plant food and insects (Soini, 1987; Terborgh, 1983). The location, identification and acquisition of food is likely to constitute one of their greatest environmental challenges. As organisms that live socially, in stable, closely-related, family troops, exhibiting high levels of co-operation and cohesion within and between species, together with a tolerant nature towards others with food (at least intra-specifically), one might expect that social learning could play an important role in how these monkeys respond to food related challenges in both single- and mixed-species troops. It is generally accepted that there is a greater likelihood of social learning in tolerant species/societies exhibiting high levels of behavioural co-ordination (Cambefort, 1981; Coussi-Korbel & Fragaszy, 1995). For example, Weigl and Hanson (1980) suggest that the intra-specific tolerance shown by *Tamiasciurus hudsonicus* (red-squirrel) in deciduous areas may be especially conducive to observational learning and the efficient exploitation of diverse seasonal food resources. More generally, they suggest that, in order to exploit diverse food resources, dietary generalists (as tamarins are) must maintain sufficient behavioural plasticity to permit the development of appropriate feeding techniques (see also Laland & Plotkin, 1990; Lefebvre *et al.*, 1996). Both asocial and social learning are forms of behavioural plasticity enabling animals to acquire behaviour adaptive to their specific habitats.

In this thesis, I investigate whether facilitation of social learning about food availability, location, quantity, palatability, and method of acquisition could constitute a potential advantage of mixed-species troop formation. If species can learn from their congeners as well as their conspecifics, then an increase in troop size as a result of association will increase the opportunity for transfer of food-related information between individuals accordingly. Furthermore, if participating species in mixed-species troops are in any way divergent in their foraging behaviour, then mixed-species troops may be at an advantage over single-species troops in that both species may potentially be able to take advantage of an increased knowledge base (i.e., that of the their own species plus that of their congeners) concerning food-related information.

Relatively few studies have focused upon social influences on the transmission of learned behaviours in ways that inform us about the contributions of social learning to group-living animals (Laland *et al.*, 1993; Adams-Curtis & Fragaszy, 1995; Coussi-Korbel & Fragaszy, 1995). This is partly because it is notoriously difficult to collect conclusive evidence for social learning in the field. It is considerably less difficult, however, in the controlled confines of the captive environment. Although individual tamarins in mixed-species troops may accrue foraging benefits in a number of ways (for example, through increased insect capture rates: Klein & Klein, 1973; Pook & Pook, 1982; Peres, 1992b; or avoidance of previously used areas: Terborgh, 1983; Buchanan-Smith, 1990a; Peres, 1992a), it is the hypothesis that species in mixed-species troops can increase their foraging efficiency by sharing or parasitising information concerning the location and nature of local food resources (Pook & Pook, 1982; Terborgh, 1983; Hardie, 1995; Peres, 1996) that lends itself most to tests in captivity. Tests with captive mixed-species troops of tamarins have previously proved useful in evaluating hypotheses regarding the costs and benefits of association. For example, Hardie (1995) was able to show that *S. labiatus* is facilitated to approach objects placed low down in an enclosure after having observed *S. fuscicollis* approaching them. He suggests that *S. labiatus* may benefit in mixed-species troops from the increased responsiveness of *S. fuscicollis* in the lower part of their environment by allowing *S. fuscicollis* to expose itself to any potential danger first and/or by displacing it should the novel object prove beneficial.

The captive environment is eminently suited to investigations of social learning. However, the majority of laboratory studies of social learning phenomena have concentrated upon underlying mechanisms, and with the exception of some ornithological studies such as those by Krebs (1973) and Rubenstein *et al.* (1977), most have examined learning within species and not between species. The experimental chapters that follow after Chapter 4 go some way towards redressing this imbalance, presenting evidence for social learning, both within and between-species, concentrating upon its functional/adaptive value in mixed-species associations, as opposed to the mechanisms by which it is achieved.

Chapter 4

Studying Captive Tamarin Troops at Belfast Zoological Gardens

> *"It takes a very long period of observing to become really familiar with an animal and to attain a deeper understanding of its behaviour; and without love for the animal itself, no observer, however patient, could ever look at it long enough to make valuable observations on its behaviour."*
>
> *[Lorenz, 1960: p. xii]*

4.1 Introduction: Testing in the Captive Environment

This thesis examines social learning and species-specific differences in foraging behaviour, with respect to the foraging advantage hypotheses proposed for the formation of tamarin mixed-species troops. As described in Chapter 1, it is extremely difficult to test these hypotheses in the wild for a number of reasons, not least because participating species are rarely found out of association. Moreover, the gathering of evidence for social learning in wild groups of animals is limited by the fact that the observations must be made at so close a distance from the animals as to be unambiguous of interpretation. It is for this reason that traditional primate field studies have neglected tests of hypotheses of social learning (although there are exceptions, e.g., Whitehead, 1986).

Investigating social learning in captivity enables experimental testing under controlled conditions. In addition, observation conditions are excellent for detailed investigations of behaviour, and the identity, age and history of individuals are known. However, traditional captive studies of social learning tell us little about how it may operate in natural populations, since in trading-off ecological validity against control, such studies fail to stimulate the full range of complex behavioural responses observable in the wild. For example, predation is rarely a real threat in the risk-limited captive environment (although captive tamarins are extremely vigilant with regards to feral cats and large, fast-flying birds, e.g., seagulls: Prescott, pers. obs.). In captivity, food is often plentiful, such that acquiring food does not require the same time investment as in the wild. Chamove and Anderson (pers. obs. in 1989) observe that captive *S. oedipus* spend less than 5 % of their time foraging. This is in sharp comparison to the amount of time wild tamarins invest in foraging for plant food and insects (approximately 60 % of their daily activity period: Terborgh, 1983; Soini, 1987, for *S. fuscicollis*). Moreover, in captivity, toxic items are usually not presented, and the food that is presented rarely requires or maintains the complex foraging strategies necessary for survival in the wild. All this means that there are few deleterious consequences of inefficient foraging in captivity and that the specific behavioural capacities necessary for acquiring, preparing and consuming food in the wild are neither developed nor maintained.

A methodological compromise to these problems is to study social learning in a semi-natural environment in captivity, where individuals can range freely and interact with their conspecifics, and in mixed-species groups, with their congeners. Such studies allow one to investigate species' propensities which may affect the dynamics of mixed-species associations, and to test functional hypotheses concerning the role of social learning in mixed-species troops, in a relatively unconstrained environment where the animal's behaviour more closely resembles that of its wild counterparts in the environment to which they are adapted.

Attention should also be paid to the nature of experimental tasks, such that study animals are tested on problems that they typically encounter in the wild, under conditions that imitate the natural learning situation. As pointed out by Fragaszy and Box (1986), with the exception of some exemplary work (Menzel, 1973; Menzel & Juno, 1982, 1984, 1985; Kamil, 1984; Garber & Dolins, 1996), most studies of learning in non-human primates have been conducted in laboratory settings with only minimal recognition of the relation between the abilities under study and the demands placed on the individual in the real world. Brown and Gass (1993) write that, in studies of learning abilities,

> *"an experimental approach that considers the ecological characteristics of a species has been instrumental in revealing capabilities considerably greater than those often expressed in standard learning paradigms"* (p. 487).

In view of this, I designed ecologically relevant learning experiments, incorporating as far as possible, the intricacies of natural tamarin foraging behaviour whilst controlling the amount of information available to the forager. Maintaining a high degree of ecological validity in all experiments enabled me to assume that the study animals, despite their captive environment, select for maximum yield, high calorific value and ease of consumption in their diets. Also, in the interest of simulating the natural environment, I further endeavoured, wherever possible, to preserve the natural foraging behaviour of the study animals by testing them in a social troop. Moreover, testing the animals together in this way provided information on a large number of individuals and yielded inductive data on the social dynamics of single- and mixed-species troops. However, most of the captive troops under observation contained fewer individuals than their natural counterparts (two to four individuals of each species, compared with a wild mean of five to seven individuals of each species; wild means calculated from the means of 19 published studies: after Hardie, 1995). This is expected to have affected the dynamics of social relationships within the troops. Where experiments necessitated the recording of detailed data from particular, single individuals, it was decided to test in male-female pairs since evidence exists that social primates perform better on several types of learning trials (e.g., spatial association tasks) when tested with a familiar companion close by (Rumbaugh *et al.*, 1989, for *P. troglodytes*; Washburn & Rumbaugh, 1991, for *M. mulatta*). Moreover, tamarins are reported to be distressed by separation from their troop-mates (Caine & Stevens, 1990, for *S. labiatus*).

It was necessary to conduct some experiments in standard, traditional indoor/outdoor zoo enclosures. The limited amount of space in such enclosures creates social restrictions which may cause stress for some troop members, due, for example, to an inability to emigrate or, for subordinate individuals, to avoid aggressive actions focused upon them. Such stresses may well have affected the behaviour of both the dominant *S. labiatus* and subordinate *S. fuscicollis*. The enclosures were, however, situated in an area off-exhibit from the public, which is likely to have reduced further stress on the study animals and which provided undisturbed conditions in which to work. Primates have been reported to be less affiliative, more excited, and more aggressive in the presence of zoo visitors, and may display an increase in stereotypical behaviour (Chamove *et al.*, 1988). However, tamarins on exhibit in zoos have shown a tendency toward inactivity and a decrease in social behaviours when compared with conspecifics housed off-exhibit (Glaston *et al.*, 1984, for *S. oedipus*).

Despite these pressures, previous work with tamarin mixed-species troops at Belfast Zoological Gardens has demonstrated behavioural patterns typical of wild tamarin associations, lending support to the generalisation of the results to other troops both in the field and in captivity. These include vertical partitioning, differential substrate use, and the dominance of *S. labiatus* over *S. fuscicollis* (Hardie *et al.*, 1993; McShane, 1995). Furthermore, it has been shown that the association in captivity is not merely a tolerance of the presence of congeners within a closed area, but that the species are actively choosing to associate as they do in the wild, remaining in close proximity (i.e., within 5 m of each other) when given the opportunity to range freely in a large wooded area approximately 550 m^2 (Hardie *et al.*, 1993; Hardie, 1997). These findings led McShane (1995) to conclude that such exhibits can be legitimately investigated to elucidate the nature of the costs and benefits of wild tamarin associations.

However, the captive situation can never be entirely indicative of the wild and one must exercise caution in drawing conclusions between field and captive studies, with regards the functional and proximate influences on behaviour in the wild. Experimental evidence that a particular factor *can* influence behaviour may not mean that the factor *does* influence the behaviour of wild individuals. This thesis seeks only to explore some of the foraging benefit hypotheses proposed for wild mixed-species troops of tamarins in captivity; to show that it is possible, for example, for one species to learn from another which foods it should eat, how to obtain certain foods, or where food is located. Evidence for learning of this kind in captivity lends support to the notion that it is possible in wild mixed-species troops, that is all. It does not provide evidence that it occurs in the wild. Moreover, it is appreciated that it is far from ideal to examine these hypotheses in isolation; for example, one ought not to examine predation and not foraging and vice-versa (see

Bshary & Noë, 1997). The proximate and ultimate causes of primate mixed-species troops are likely to be many and to form part of a complex cost-benefit analysis in which the costs and benefits may be different for each species and for individuals within each species. However, testing in captivity can help us confirm, reject, refine or adapt existing field hypotheses proposed for the function of tamarin mixed-species troops, and can aid in the generation of new ones, for relating back to concurrent data from the field. The convergence of these two parallel lines of enquiry is likely to represent the most fruitful approach to answering the question: why do tamarins form mixed-species troops?

4.2 The Testing Paradigm

In view of the problems associated with testing hypotheses concerned with the costs and benefits of tamarin mixed-species associations in the wild (see Section 2.7), Buchanan-Smith and Hardie (1997) derived a paradigm for testing the mixed-species troops they had created in captivity. The paradigm compares and contrasts the behaviour of each species in the presence and absence of its congener, which helps clarify the costs and benefits of association to each species. It is necessary to demonstrate that individuals in mixed-species troops actually benefit from associating when compared to alternative strategies, such as living independently of each other or forming similarly-sized single-species troops. The paradigm is of either a within-subject or between-subject design.

In the within-subject design, comparisons are made between individuals in single-species troops with those *same* individuals in mixed-species troops. The design is advantageous in that it allows examination of the direct effect of the presence of the congener on the behaviour of particular individuals. However, a design of this type is confounded by troop size, in that, it is not possible to determine whether any observed effects are due to the increase in troop size resulting from the formation of the mixed-species troop from two single-species troops, or whether they are directly related to the propensities of the associating species.

In the between-subject design, comparisons are made between single-species troops containing the same number of individuals as the combined number of both species in an analogous mixed-species troop. The adoption of this approach is made difficult by the social organisation and breeding system of tamarins, in that, it is not possible to match the sex and age troop composition of the mixed-species troop with those of the respective single-species troops by forming troops of unrelated conspecific individuals due to aggression. It is possible to use a single-species family and compare it with a mixed-species troop of the same size, but care must be taken to ensure such family troops have a similar age composition to the mixed-species troop, or else interpretation of the results will be confounded. The experiments contained in this thesis are of both designs.

4.3 Study Animals

Study animals were troops of two species of tamarin monkey, *S. fuscicollis weddelli* (Weddell's saddle-back tamarin) and *S. labiatus labiatus* (red-bellied tamarin or Geoffroy's moustached tamarin), housed at Belfast Zoological Gardens, Belfast, Northern Ireland. Most individuals were captive born. Eleven troops of *S. fuscicollis* and eleven troops of *S. labiatus* were studied over the course of the study. Each troop consisted of an adult male-female pairing (most often a monogamous breeding pair), and approximately half of these lived together with one or two generations of offspring. Troop composition sometimes changed over the course of the study, either due to births, deaths, or due to re-arranging for breeding or experimentation. The first phase of experimentation began in April, 1996, and was completed in the September of that year. A second phase began in April, 1997, and was completed in September, 1997. Experimentation was conducted in the spring and summer months only because in the autumn and winter the tamarins are relatively inactive and spend much of their time indoors, or else huddling to keep warm whilst outdoors. Details concerning the grouping, sex, age and relatedness of individuals within the troops studied in the first summer are given in Tables 4.1 and 4.2, and in the second summer, Tables 4.3 and 4.4.

Most experiments involved testing these troops as single-species troops and as mixed-species troops, created by careful mixing of troops of each species. Details of the procedure used are given below (Section 4.7) courtesy of Hardie (1995, 1997). Some troops had been housed as mixed-species troops previous to the start of experimentation. Study animals were not artificially marked or collared for individual identification because individuals were recognisable by virtue of their body size and distinctive facial and body markings. Information on idiosyncratic behaviours was collected *ad libitum*.

4.4 Age Categories

Since age was a factor considered in the analysis of Experiments 1, 2 and 3, a criterion for deciding the developmental state of study animals was required in order to correctly assign individuals to separate age categories. Previous authors have used a number of criteria, depending upon their personal preference and the species under study (see Neyman, 1978, 1980; Cleveland & Snowdon, 1984; Price, 1990a; Yamamoto, 1993). Generally, criteria are based around the inter-birth interval (IBI) and age of onset of sexual

Table 4.1: Details of grouping, sex, age and relatedness of *S. fuscicollis* study animals at Belfast Zoological Gardens during the first summer of data collection (April to September, 1996).

Troop	Males	I.D.	Date of Birth	Females	I.D.	Date of Birth
SF1	Adult male	#217	05/11/87	Adult female	#778	26/05/92
	Son	#1498	29/04/95	Daughter	#1497	29/04/95
	Son	#2160	12/05/96	Daughter	#2159	12/05/96
SF2	Adult male	#474	05/06/90	Adult female	#742	16/03/93
	Son	#1483	17/04/95			
SF3	Adult male	#780	21/02/93	Adult female	#743	16/03/93
SF4	Adult male	#779	26/05/92	Adult female	#926	22/03/94
				Daughter	#2334	12/07/96
SF5	Adult male	#989	04/08/90	Adult female	#1045	29/05/91
				Daughter	#2214	20/05/96
SF6	Adult male	#744	20/09/90	Adult female	#2215	24/05/86
SF7	Adult male	#1483	17/04/95	Adult female	#2216	24/05/86
SF8	Adult male	#776	12/11/89	Adult female	#223	06/01/89
	Son	#2002	31/10/95	Daughter	#2003	31/10/95

Table 4.2: Details of age, sex and grouping of *S. labiatus* study animals at Belfast Zoological Gardens during the first summer of data collection (April to September, 1996).

Troop	Males	I.D.	Date of Birth	Females	I.D.	Date of Birth
SL1	Adult male	#874	01/05/91	Adult female	#888	22/06/92
	Son	#1500	30/04/95	Daughter	#1499	30/04/95
	Son	#2289	16/06/96	Daughter	#2290	16/06/96
SL2	Adult male	#656	10/02/91	Adult female	#1384	09/05/93
SL3	Adult male	#872	01/01/93	Adult female	#868	28/05/90
SL4	Adult male	#871	09/06/83	Adult female	#657	30/11/91
	Son	#2335	16/07/96	Daughter	#2336	16/07/96
SL5	Adult male	#1708	01/08/92	Adult female	#1707	01/08/92
SL6	Adult male	#664	10/05/89	Adult female	#665	20/09/90
	Son	#2346	23/07/96	Daughter	#2345	23/07/96
SL7	Adult male	#2310	29/05/92	Adult female	#2311	08/06/89
SL8	Adult male	#2306	29/05/92	Adult female	#2307	10/01/91
	Juvenile male	#2309	07/11/95	Juvenile female	#2308	07/11/95

Table 4.3: Details of grouping, sex, age and relatedness of *S. fuscicollis* study animals at Belfast Zoological Gardens during the second summer of data collection (April to September, 1997).

Troop	**Males**	**I.D.**	**Date of Birth**	**Females**	**I.D.**	**Date of Birth**
SF2	Adult male	#474	05/06/90	Adult female	#742	16/03/93
				Daughter	#2225	31/05/96
				Daughter	#2426	12/11/96
				Daughter	#2427	12/11/96
SF3	Adult male	#780	21/02/93	Adult female	#743	16/03/93
	Son	#2365	25/08/96	Daughter	#2364	25/08/96
SF4	Adult male	#779	26/05/92	Adult female	#926	22/03/94
				Daughter	#2334	12/07/96
SF5	Adult male	#989	04/08/90	Adult female	#1045	29/05/91
				Daughter	#2214	20/05/96
	?	#2421	10/11/96	?	#2422	10/11/96
SF6	Adult male	#744	20/09/90	Adult female	#2215	24/05/86
				Daughter	#2583	25/01/97
				Daughter	#2584	25/01/97
SF7	Adult male	#2002	31/10/95	Adult female	#1497	29/04/95
SF9	Adult male	#1498	29/04/95	Adult female	#2003	31/10/95
SF10	Adult male	#217	05/11/87	Adult female	#778	26/05/92
	Son	#2160	12/04/96	Daughter	#2159	12/04/96
SF11	Adult male	#1483	17/04/95	Adult female	#223	06/01/89

Table 4.4: Details of age, sex and grouping of *S. labiatus* study animals at Belfast Zoological Gardens during the second summer of data collection (April to September, 1997).

Troop	Males	I.D.	Date of Birth	Females	I.D.	Date of Birth
SL2	Adult male	#656	10/02/91	Adult female	#1384	09/05/93
SL3	Adult male	#872	01/01/93	Adult female	#868	28/05/90
SL4	Adult male	#871	09/06/83	Adult female	#657	30/11/91
	Son	#2335	16/07/96	Daughter	#2336	16/07/96
SL5	Adult male	#1708	01/08/92	Adult female	#1707	01/08/92
				Daughter	#2408	24/10/96
SL6	Adult male	#664	10/05/89	Adult female	#665	20/09/90
	Son	#2346	23/07/96	Daughter	#2345	23/07/96
SL7	Adult male	#2306	29/05/92	Adult female	#2311	08/06/89
SL9	Adult male	#1500	30/04/95	Adult female	#2308	07/11/95
SL10	Adult male	#874	01/05/91	Adult female	#888	22/06/92
SL11	Adult male	#2306	29/05/95	Adult female	#2307	10/01/91

maturity of the species under study. The IBI of wild and captive tamarin individuals has been reported to differ (Wolfe *et al.*, 1975). For captive *S. fuscicollis*, the average IBI is approximately 220 - 250 days (Snowdon & Soini, 1988; Buchanan-Smith *et al.*, 1996), while wild populations may breed only once a year (thus increasing the IBI) (Goldizen *et al.*, 1988). The average IBI for captive *S. labiatus* is 165 - 182 days (Ogden & Wolfe, 1979; Buchanan-Smith *et al.*, 1996) with again probably a yearly birth interval in the wild. The age of onset of sexual maturity in captive *S. fuscicollis* can be as early as 12 months or less (Epple & Katz, 1980). The exact age of onset of sexual maturity in the wild is unclear. In view of this, Goldizen & Terborgh (1989) suggest that sexual maturity in wild *S. fuscicollis* can be assumed at 18 - 24 months. A lack of equivalent data for *S. labiatus* necessitates the use of this criterion for *S. labiatus* also.

The following age categories were used:

Infant	0 - 6 months (based on minimal IBI)
Juvenile	6 - 12 months (based on yearly IBI in wild)
Sub-adult	12 - 18 months (age until possible sexual maturity)
Adult	18 + months (complete sexual and physical maturity)

4.5 Records

Details of all individual animals at the zoo, were stored as computer records in the ARKS management and record computer-program. The records contained information concerning sex, age, parentage, place of birth, dates of pairings, deaths and births etc. In addition to this, a daily journal of unusual or interesting events (e.g., matings, excessive aggression) was kept in the 'Old Marmoset-House' by myself and the keepers. Together, these information databases provided an accurate record of events concerning the study animals, even in my absence.

4.6 Housing and Husbandry

The study animals were housed and tested in three environments, all of which were situated in the 'old-zoo', an off-exhibit area, closed to the public, and used to house quarantined and surplus animals. Detailed descriptions of these three environments are given below. At any one time, seven troops of *S. fuscicollis* and seven troops of *S. labiatus* were housed in the 'Old Marmoset-House', together with a number of other callitrichine species (*S. mystax, S. imperator, S. oedipus, S. bicolor, C. jacchus, C. geoffroyi* (Geoffroy's tufted-ear marmoset), *L. rosalia, Callimico*) and alongside a series of bird cages containing parrots, macaws, cockatoo, ibis, cranes, and fowl. The 'Free-Range Area' contained, at any one time, only a male-female pair of each species and their dependent, infant offspring.

4.6.1 Old Marmoset-House

The 'Old Marmoset-House' consisted of twenty standard, captive indoor/outdoor enclosures, ten on the left side of a central corridor (numbered C1 - C10) and eight on the right (C11 - C18), and a large 'End-Enclosure'. The layout is illustrated in Figure 4.1. Single-species troops occupied a single indoor/outdoor enclosure; mixed-species troops occupied two of these. Species in mixed-species troops were fed together in one of their two enclosures and either slept together or in separate enclosures as they wished.

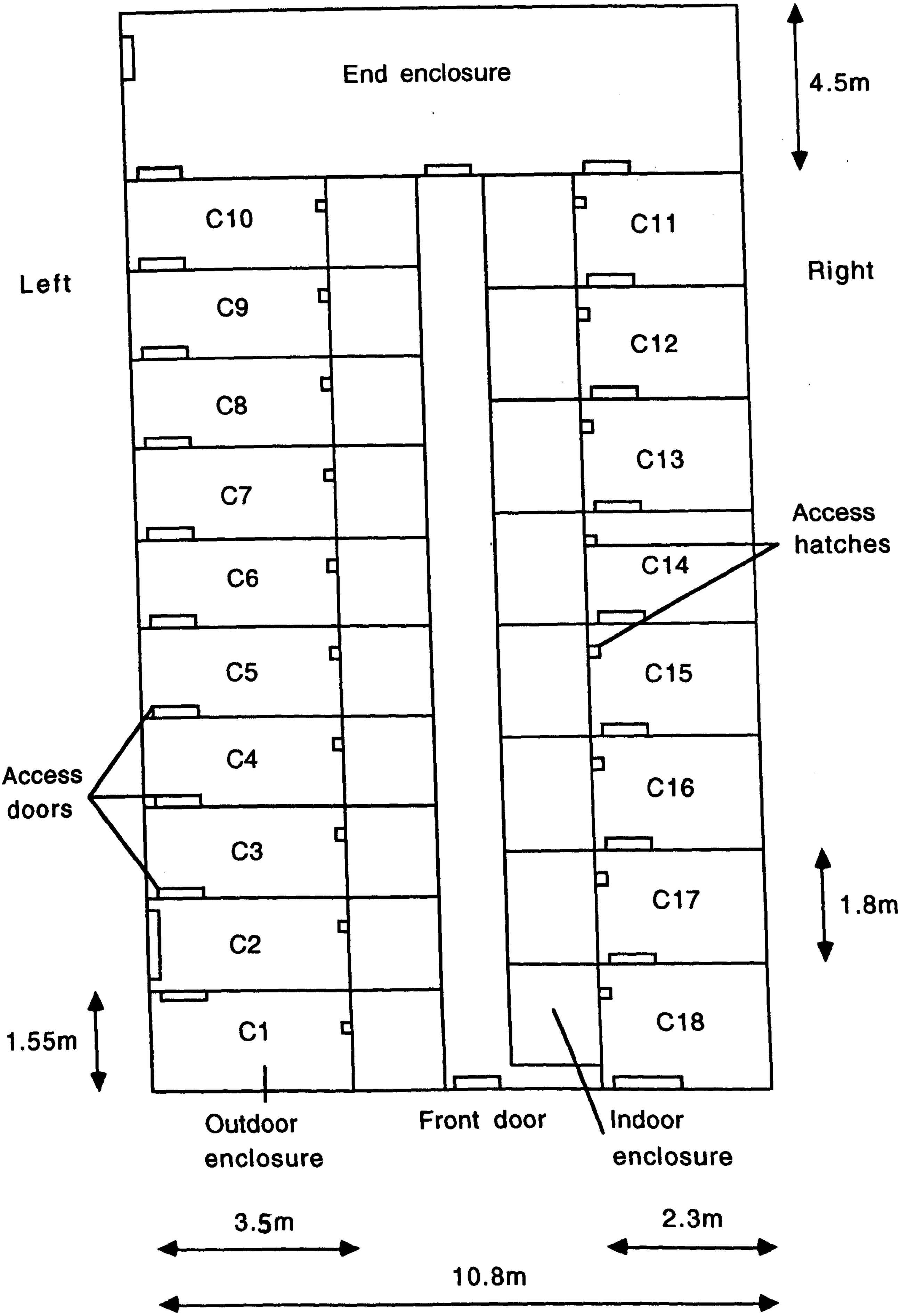


Figure 4.1: Schematic Plan of the 'Old Marmoset-House' (not shown to scale).

The right-hand side enclosures consisted of:

(a) An indoor area, measuring approximately 2 x 1.75 x 1.5 m, furnished with a concrete floor, covered with wood-shavings, and a network of approximately four medium-sized (5 - 10 cm diameter) branches for locomotion. The branches were positioned between a closeable access hatch (30 x 30 cm), which allowed access to the outside area, and the floor of the indoor area. Each indoor area contained a shelf and one or more plywood nest-boxes for resting and sleeping (30 x 25 x 25 cm), either affixed to the wall or placed upon the shelf.

(b) An outdoor area measuring approximately 1.9 x 1.8 x 2.3 m, bounded by a wooden frame covered with 1 cm^2 plastic netting, and furnished with a network of approximately eight medium- to large-sized branches (5 to >10 cm in diameter). The floors of the outside areas were covered with soil and wood-chips and supported grass and live shrubbery. Adjacent outdoor areas were separated by a double wall of 1cm^2 wire netting with a 3 cm gap between, effectively preventing physical access (but allowing visual, auditory and olfactory contact) between monkeys in adjacent enclosures (Plate 3). Access between adjacent enclosures, for the keepers and myself, was through access doors (1.8 x 0.87 m) in the sides of the outdoor area walls (see Figure 4.1).

The left-hand side enclosures were much the same in style and content as the right-hand enclosures but had smaller (1.65 x 1.55 x 1.5 m), similarly-furnished indoor areas and slightly larger outdoor areas (1.95 x 1.55 x 3.5 m). The floor of the indoor areas was raised approximately 1 m from the floor of central corridor. All indoor areas were thermostatically controlled and had a heatlamp and a heater under each shelf. The

Plate 3: The 'Old Marmoset-House' at Belfast Zoological Gardens, showing the adjacent outdoor areas of the tamarins' enclosures. The 'End-Enclosure' can be seen at the far end of the House.

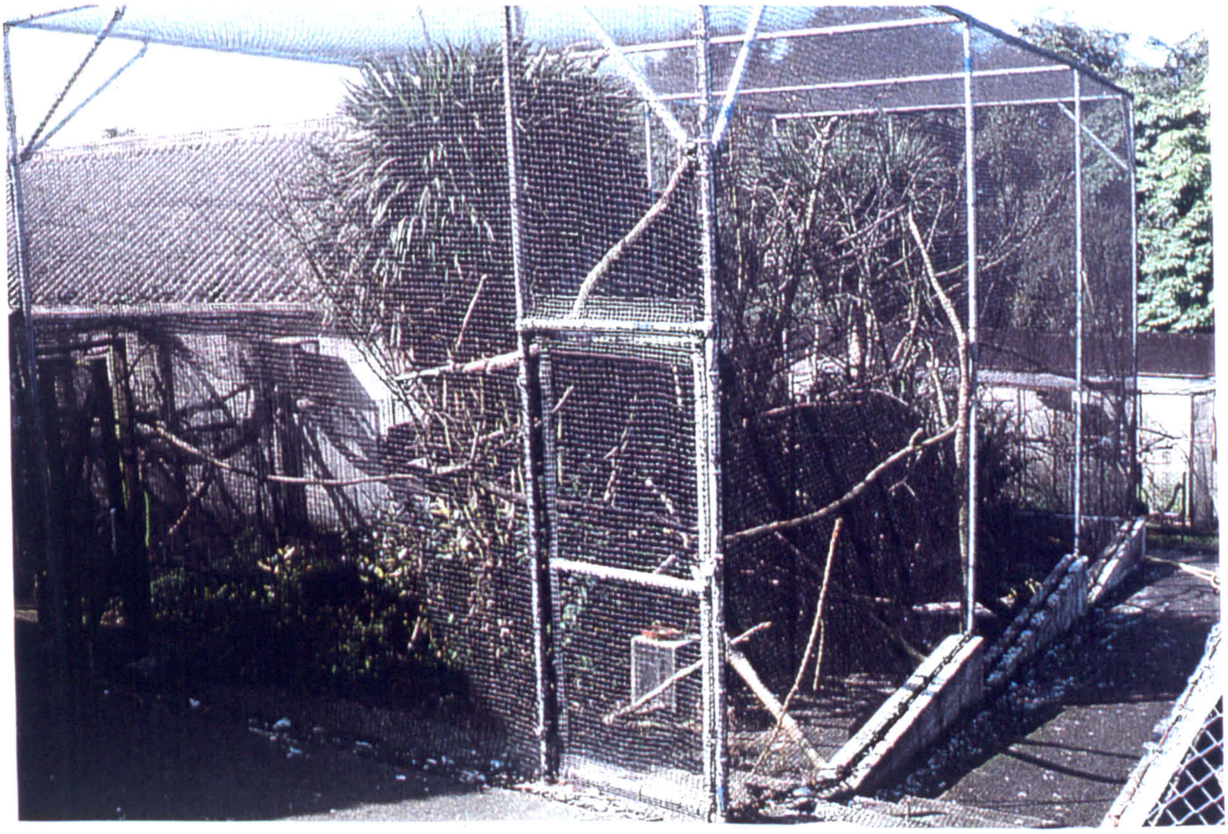


Plate 4: The 'End-Enclosure' of the 'Old Marmoset-House'.

temperature was maintained at 20 - 25 °C all year round. Lighting was provided by artificial strips between 0800 and 1600 hours. Natural light entered through the access hatches connecting the indoor and outdoor areas. The monkeys were allowed free access between the indoor and outdoor areas, except for routine husbandry and for those parts of the study when experimental protocol dictated otherwise. The indoor areas were cleaned thoroughly each day, and fresh wood shavings scattered on the floor. Freshly prepared fruit and vegetables, along with primate pellets, were given once daily, usually before 1230 hours. In addition, the monkeys received a protein element in their diet (marmoset jelly, eggs, chicken, or crickets) which was varied over each week. Food was placed in dishes on the floor of the indoor areas, or on the aforementioned resting/sleeping shelf. Vitamin supplements were given on a regular basis (generally multivitamins) and Milupa™ infant food was supplied for nursing females. Finally, fresh water was provided daily in a bowl on the floor of the indoor areas.

4.6.2 End-Enclosure

The 'End-Enclosure' consisted of an area (4.5 x 10.8 m) bounded by a metal framework covered with 2.5 cm^2, plastic mesh netting (Plate 4). The enclosure floor was inclined left to right. This meant that the enclosure was 5 m high at its left-hand side and 3.7 m at its right. Two semi-circular shrub beds (approximately 3 m in diameter), each containing shrubs and one palm tree approximately 4 to 5 m in height, were situated to the left and right of the enclosure. Outwith these shrubbed areas, the ground was covered with bare concrete. The enclosure was furnished with an approximately equal number of horizontal, vertical and oblique branches of various sizes (<5 to >10 cm in diameter) built into a semi-sturdy network, with the thin branches intermingled together, in order to create an artificial ‘canopy’ at a height of 2.5 to 3 m. The monkeys gained access to the ‘End Enclosure’ via doors (1.8 x 0.78 m) in each of the adjoining home enclosures (C10 and C11) (see Figure 4.1). Horizontally-orientated large branches (>10 cm diameter), at an intermediate height in the enclosure, provided a solid ‘runway’ by which the monkeys could enter (without having to descend to the floor) and traverse the whole enclosure from C10 to C11.

4.6.3 Free-Range Area

The ‘Free-Range Area’ consisted of a wooded and turfed, steeply inclined area approximately 60 m by 40 m (Figure 4.2) (Plate 5). Upon the turfed area, and facing the wooded area, were two adjacent home enclosures (4.6 x 3.1 x 2.5 m) (Plate 6). The enclosures were constructed from a wooden frame to which either 1 cm^2 plastic netting (Enclosure A) or 2.5 cm^2 plastic netting (Enclosure B) was attached. Each enclosure contained a wooden platform (1.5 x 1.5 m) raised, at its centre, approximately 1 m from the inclined ground. Upon each was a centrally placed, heated and insulated wooden kennel (0.5 x 0.7 x 1 m) for sleeping and protection from the elements (Plate 7). The enclosures also contained a semi-sturdy network of medium- to large-sized branches (5 to >10 cm) upon which the monkeys were able to locomote. These were attached to enclosure frame, the platform, nest boxes, and to each other, using staples and strong twine, to provide as rich and complex a home environment as possible. In addition, two wooden planks were placed beneath the platforms enabling the animals to locomote on the ground without having to negotiate the uneven, inclined surface, which they appeared to dislike. The right-hand enclosure (Enclosure B) was built around a large birch tree. There were various branches attached between the tree and the platform in this enclosure. In order that the

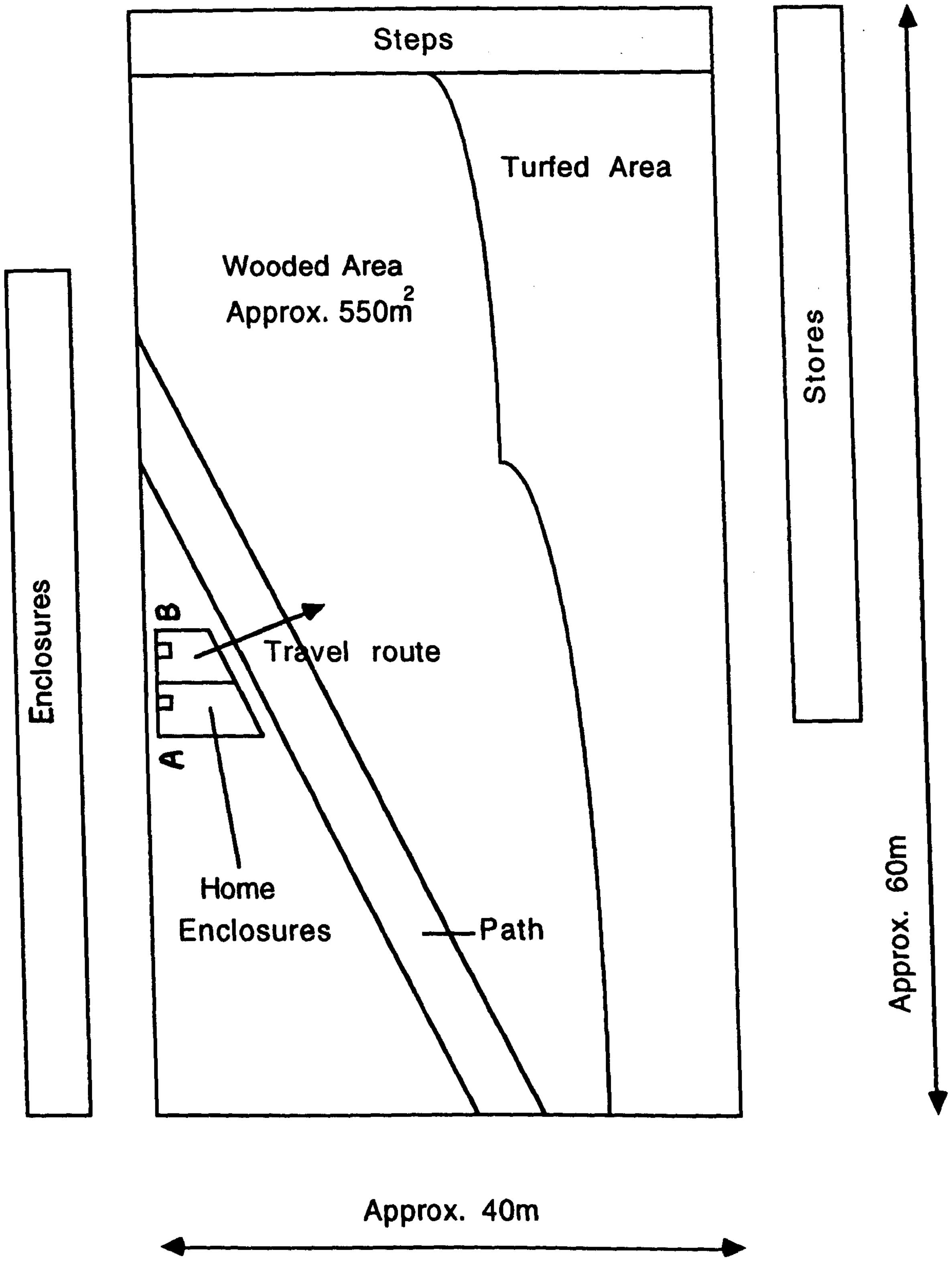


Figure 4.2: Schematic plan of the 'Free-Range Area' (not shown to scale).

Plate 5: The wooded and turfed 'Free-Range Area' at Belfast Zoological Gardens.

Plate 6: The adjacent home enclosures from which the tamarins gained access to the wooded 'Free-Range Area' (visible on the right).

Plate 7: A wooden kennel in a home enclosure on the 'Free-Range Area'. Note the access hatch (top left) through which the tamarins gained access to the wooded area (in the background).

monkeys may have free access to the wooded area, without having to descend to the ground, a closeable access hatch was situated in the top left-hand (Enclosure B), and top right-hand (Enclosure A), of the enclosure sides facing the wooded area. Branches ran from the central network to these access hatches. From the hatches the monkeys could reach the roofs of the home enclosures, and thenceforth the branches of the tree, surrounding Enclosure B, that lead into the trees of the wooded area. The monkeys were allowed free access to the wooded area, except when experimental protocol dictated otherwise. The kennel and platform in each enclosure were cleaned daily and the monkeys provided with food and water in exactly the same manner as that for the monkeys housed in the 'Old Marmoset-House'.

4.7 Mixing Protocol

The creation of the mixed-species troops was conducted according to a systematic protocol devised by Hardie (1995, 1997) and generally took place in the 'End-Enclosure'. The protocol consisted of first housing a single-species troop of each species in the separate enclosures that adjoin the 'End-Enclosure' (C10 and C11). The congeneric single-species troops were then given daily access to the 'End-Enclosure', alternately, in order for them to become familiar with the enclosure and lay-down scent in this novel 'territory'. Alternate access to this area also allowed visual, auditory and olfactory contact between the species, through the enclosure sides that join C10 and C11 to the 'End-Enclosure', prior to physical introduction. Attention was paid to the amount of time individuals of each species spent looking at each other (as a means of gauging interest between species: McGrew & McLuckie, 1986; Moore, *et al.*, 1991), scent marking, alarm-calling and agonistic behaviour. After a period of at least three days, simultaneous, free-access to the 'End-

Enclosure' was given to both species. Again, the procedure was monitored carefully. Specifically, this involved estimating the level of interest the species had in each other, scent-marking, alarm-calling, pilo-erection and agonistic behaviour.

An indication as to whether the mixing attempt was likely to be successful could usually be gained in the first few crucial hours. Generally, there were relatively few interactions between species, and these were usually non-hostile. If aggression did occur, it was most often centred around a dispute over food. The newly-formed mixed-species troop was observed periodically over the following weeks in case of problems. Although an elaborate introduction is not necessary, it is thought that mixing in an area novel to both species reduces the likelihood of territorial conflict. Moreover, if the mixing-enclosure is large, individuals are able to abscond in the event of aggression (Hardie *et al.*, 1993). Callitrichine species have been found to habituate quickly to changes in their physical environment (e.g., Menzel & Menzel, 1979, for *S. fuscicollis*; Box, 1984, for *C. jacchus*), and following relocation to new enclosures for mixing or testing, the study animals were observed to settle down very quickly (a 3 to 7 day adjustment period was always allowed before the commencement of testing). At Belfast, both *S. fuscicollis* and *S. labiatus* have bred and reared young successfully in the mixed-species troops, but inter-specific aggression around the time of births sometimes necessitates intervention and separation.

4.8 Experimental Food Items

Following a general food preference test (offering sultanas, raisins, shelled peanuts, mealworms, quartered grapes, or eighthed glace cherries) it was decided that mealworms (larval stages of the flour beetle, *Tenebrio mollitor*) were to be used as food items in all experiments (except for Experiments 1, 2 and 3). Mealworms were chosen as they were well-liked, elicited little bias (sex, species, troop, or individual) in the food preference tests, were of uniform size, were relatively clean in that they did not stick to the wood shavings used in the experiments, and a cheap, reliable, self-perpetuating supply was readily available once a colony was set up. In order to simulate natural conditions, food items were always presented in elevated positions, accessible to the monkeys only by climbing upon or leaping between supports.

4.9 Observation Protocol, Data Collection and Sampling Methods

4.9.1 Observation Protocol

Troops were tested in all three of the environments described in Section 4.6, depending upon experiment. Testing was generally conducted outdoors, with the exception of Experiments 2 and 3, which were conducted indoors. During data collection, unless the study animals were out of sight, I remained seated some 2 metres from the front of the testing enclosure. All animals were well habituated to my presence and usually paid me no concern.

4.9.2 Data Collection

Four different recording methods were used depending upon the particular needs of the different experiments:

(a) Checksheets

For food preference trials and simple experiments, checksheets were used. These were designed according to the recommendations of Hinde (1973), and Martin and Bateson (1986). They were most often used in conjunction with a time sampling strategy. Time was denoted by a stopwatch, and sample intervals by an electronic metronome, audible only to myself.

(b) Hand-held computer

For experiments in which it was necessary to systematically record all instances of a few particular behaviours, and the precise latency with which these were performed, I used a hand-held computer running THE OBSERVER 3.0 event recording computer-program (Noldus, 1993). THE OBSERVER 3.0 records the latencies with which particular behaviours are performed automatically as one keys the behaviours into the computer. An adequate degree of competence on the computer was reached for all experiments during pilot runs before testing commenced.

(c) Miniature tape-recorder

For experiments requiring the recording of a range of behaviours, together with any associated contextual information and the latency with which the behaviours were performed, and for those requiring the recording of the instantaneous behaviour of a number of individuals by scanning, I used a miniature tape-recorder (into which I dictated a record of the behaviours observed). Both methods (b) and (c) enabled me to collect data whilst keeping my eyes continuously on the study animals.

(d) Video-camera

For Experiments 2 and 3, it was necessary to use a video-camera as well as a miniature tape-recorder, because I wished to record the simultaneous behaviour of a number of individuals in detail at more than one locality. The use of tape-recorder and video-camera for data collection meant that a considerable amount of time was devoted to transcribing audio- and video-tapes in the evenings.

4.9.3 Sampling Methods

Due to the potentially large number of study animals under observation in some experiments it was deemed inappropriate to record behaviour *ad libitum* and instead necessary to adopt a sampling strategy. The sampling strategy used varied according to the needs of the experiment but was most often behavioural sampling or scan sampling (Martin & Bateson, 1986). Mutually exclusive behavioural categories used to define the behaviour of the study animals are given in Table 4.5. The recording rule used to record behaviour also differed between experiments and was either 'all-occurrences' recording (Altmann, 1974), 'instantaneous time sampling' or 'one-zero sampling' (Martin & Bateson, 1986). Further details are provided in the recording methods section of each experiment.

Circadian rhythms in activity and behaviour have been noted in many studies of tamarins (e.g., Neyman, 1978; Garber, 1980; Pook & Pook, 1982) and could have potentially affected the results of this study. To control for these, observation sessions were balanced between troops for time of day. All observation sessions were split equally between morning (0900 - 1230 h) and afternoon (1330 - 1630 h), unless stated otherwise.

Table 4.5: Mutually exclusive behavioural categories used to define activity of the tamarins (Based on Garber, 1980, 1984; Coates & Poole, 1983; Buchanan-Smith, 1989; Price 1990a; Hardie, 1995).

Behaviour	**Definition**
Look	Animal stationary, with fixation of stare on object or animal.
Look Up	A deliberate single head movement upwards, or static stare in an upward direction with head usually angled 45° from the horizontal.
Scan	Scanning head movements from side to side and/or up and down in a continuous flux of movement.
Forage/Search	Animal searches, by manipulating substrates or by visual inspection, through area in an attempt to gain plant or insect food item.
Eat	Consume any type of food item.
Rest	Stay still and relaxed in any posture (does not include any other behaviour, e.g., groom, huddle etc.).
Huddle	Stationary contact with another, where torso and/or limbs are touching (does not include any other behaviour).
Allo-Groom	Individual picks through pelage of another, with visual inspection and parting of fur by hand(s) or mouth.
Auto-Groom	Individual picks through its own pelage, with visual inspection and parting of fur by hand(s) or mouth.
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 gives characteristic alarm call and acts in an alarmed manner.
Food Call	Animal gives characteristic food call upon encountering food.
Call	Utter any type of vocalisation other than alarm- or food-call.
Scent Mark	Animal performs an act of depositing scent and/or urine upon a substrate. Either anogenital, suprapubic, or sternal.

Food Transfer	Animal allows another to take food from its mouth or hand without resistance.
Food Steal	Animal takes food forcibly from the mouth or hand of another, with resistance from that other.
Agonistic Behaviour	Aggressive contact (e.g., cuffs, grabs, slaps, bites) or non-contact (e.g., stares, lunges, open-mouth lunges, chases, head-shakes, tongue-flicking) and approaches (i.e., animal approaches to within 15 cm of, or passes close by, another which leads to displacement of that other, regardless of whether it is accompanied by aggression).
Displacement	Animal directly withdraws from the approach of another.
Copulation	Sexual intercourse where penetration has occurred.
Solicitation	Attempt by male to copulate.
Other	Any behavioural pattern not otherwise listed (e.g., nursing etc.).

The behavioural repertoire of various species of *Saguinus* has been categorised by several authors (Vogt, 1978, for *S. fuscicollis*; Coates & Poole, 1983, for *S. labiatus*; Garber, 1980; Price, 1990a, for *S. oedipus*). No agreed ethogram of behaviour exists, and while each set of behavioural definitions are globally similar, they have been adapted to suit the needs of each researcher. In the present study, previously used definitions were adopted where appropriate, otherwise definitions were formulated to suit the purposes of each experiment.

Chapter 5

Social Learning About Food Acquisition

"Social learning in animals might best be described as socially biased individual learning".

[Galef, 1996c: p. 641]

5.1 Introduction

Chapter 3 described how social learning may be adaptive if it allows animals to deal with difficult foods (those requiring processing) rapidly and effectively without making costly mistakes or wasting time in exploration or sampling. Social learning of this kind may apply to tamarins in the wild in as much as their diet consists, in the main, of insects and ripe fruit, both of which may require processing. The most important insect prey (indeed, animal prey) for tamarins are orthopterans. They are reported to account for between 61 % and 82 % of all identified animal prey for *S. fuscicollis* (Terborgh, 1983; Crandlemire-Sacco, 1986; Peres, 1993b), 57 % for *S. imperator* (Terborgh, 1983) and 68 % for *S. mystax* (Peres, 1993b).

Several species of orthopterans possess strong mandibles capable of delivering a painful bite to their attackers. Tamarins almost invariably deal with such prey by delivering a crushing bite to head capsule of the insect, thereby disabling and immobilising it with their long, sharp canines, and thus avoiding being bitten (Nickle & Heymann, 1996; Prescott, pers. obs.). It is possible that, during development, individuals must learn how to properly subdue such prey in this way. In addition to formidable physical defences, such as biting mouth-parts, spines or pinching legs, some species of orthopteran employ crypsis or concealment strategies which must be overcome for successful capture (Robinson, 1969;

Belwood, 1990; Nickle & Heymann, 1996). Others exhibit aposematic colouration or patterning, the significance of which, either truthfully or falsely indicating toxicity, must also be learnt if emetic experiences are to be avoided.

The remainder of the insect prey taken by tamarins are mostly lepidopterans (moths and butterflies) (Terborgh, 1983; Peres, 1993b). Lepidopteran caterpillars may possess irritating urticating hairs or spines, and both the orthopteran and lepidopteran larval and adult forms may also possess chemical defences, either manufactured by themselves or sequestered from their plant foods (O'Toole, 1995). Tamarins also take arachnids (spiders) which possess biting mandibles, some possess urticating hairs, and some are venomous. Insect (and arthropod) prey thus represents a considerable challenge for foraging tamarins, one element of which is the deployment of sophisticated motor skills for successful, safe exploitation. Plant foods may also require extensive processing (e.g., fruits guarded by spine or thorns). However, the plant resources taken by tamarins appear to present them with little difficulty. Most fruit eating involves little in the way of manipulation other than the gathering of the fruit with mouth or hands. This may be a problem, though, for the small-sized fruit resources, often taken by tamarins, which are situated on the thin terminal branches of trees, and for the heavy pendulous pods of *Parkia* species, from which tamarins lick exuding resin, that are suspended on long thin stalks (Plates 8 and 9). Both of these resources must be reached using a particular '*grasping*' strategy (Hardie, 1998; Prescott, pers. obs.).

In order to exploit their diverse diet then, tamarins have to learn not only which food items are safe to eat (their stimulus characteristics), but also how these items are to be acquired and processed quickly and efficiently. One might expect that there would be

Plate 8: Some common foods of tamarins, showing the elongate pods of *Parkia* (top right).

Plate 9: Elongate pendulate pods of *Parkia* hanging from their long, thin stalks.

considerable selective pressure to acquire this information for survival. If naïve individuals can do this more quickly and safely by observing experienced others than by independent, asocial learning (or if they are facilitated to acquire this information for themselves more quickly as a result of interaction with experienced others), then social learning will be an adaptive strategy. As described in Chapter 3, living as they do in cohesive, co-operative extended family troops, tamarins are provided with numerous opportunities for social learning to occur. Furthermore, if species are able to learn from their congeners as well as their conspecifics, then association, through an increase in troop size, will increase the opportunity for information transfer between individuals accordingly. In wishing to explore this proposition, I designed an ecologically relevant novel foraging task to examine whether improved food acquisition, through social learning, is a potential advantage of mixed-species troop formation.

5.2 Experiment 1: Intra- and Inter-Specific Social Learning of a Novel Foraging Task

The aim of this experiment was to investigate whether the presence of a conspecific or a congener has any influence on the rate at which an individual learns how to access food in a novel foraging task. The hypothesis is that the opportunity to learn from another experienced individual (social learning) will result in faster acquisition of the necessary information to succeed on the task than will independent (asocial) learning.

5.2.1 Study Animals

The study animals were adult male-female pairs and their eldest male and eldest female offspring (juveniles or sub-adults) taken from three troops of *S. fuscicollis* (SF1, SF8: Table 4.1; SF10: Table 4.3) and three troops of *S. labiatus* (SL1, SL8: Table 4.2; SL6: Table 4.4); and adult, juvenile or sub-adult male-female pairs taken from five troops of *S. fuscicollis* (SF3, SF6: Table 4.1; SF2, SF4, SF5: Table 4.3) and five troops of *S. labiatus* (SL3, SL7: Table 4.2; SL2, SL4, SL5: Table 4.4). All troops were housed in separate indoor/outdoor enclosures in the 'Old-Marmoset House'. Further details of housing and husbandry are given in Chapter 4 (Section 4.6). The troops for the inter-specific condition (see Section 5.2.3) were normally maintained as mixed-species troops (SF3 & SL3, SF6 & SL7, SF2 & SL2, SF4 & SL4, SF5 & SL5) and were separated into adjacent enclosures only when necessary according to the experimental protocol. The sixth inter-specific pairing was made from individuals drawn from SF3 (#2364 & #2365: Table 4.3) and SL4 (#2335 & #2336: Table 4.4). The monkeys' ages were similar across species and ranged from 1 year to 13 years at the time of testing.

5.2.2 The Foraging Task

The tamarins were required to learn how to obtain pieces of banana, a highly preferred food, suspended from the roofs of their enclosures by lengths of string. This task was considered to be a novel one for the tamarins, in that they had not previously been presented with food in this way and had no previous experience with this type of apparatus, but it is related to the foraging behaviour of the species in the wild. In their natural habitat, tamarins take mainly small-sized or pod-like fruit resources which are situated on the terminal branches of the periphery of the tree crown (e.g., *Inga* spp., *Brosimum* spp., *Pourouma* spp.) or else hang down from moderate-sized branches (e.g., *Cecropia* spp.) (Crandlemire-Sacco, 1986; Garber, 1986, 1987, 1988a,b; Hardie, 1998, for *S. fuscicollis*; Yoneda, 1981, 1984b; Hardie, 1998, for *S. labiatus*). These terminal branches are not sturdy enough to support an upright stance (indeed, their thinness probably prohibits larger primate competitors from utilising these resources), so in order that they may reach the fruit, the tamarins adopt a '*grasping*' strategy whereby they hang upside down, suspended from the thin branches of the tree, usually by their legs only, but occasionally also using one of their arms, leaving the hands and mouth free for manipulation of the fruit (Hardie, 1998; Prescott, pers. obs.). This strategy is also used to access the pendulous pods of *Parkia* species, the pods being too rigid and long to be pulled upwards easily by the tamarins.

The behavioural components required to reach the food item in the experimental task were very similar to this grasping strategy. In order to obtain the food item, it was necessary for the monkeys to climb up one of the mesh enclosure sides to the mesh roof, locomote by quadrapedal suspension across it, and upon reaching the string, pull it up with their hands whilst hanging bipedally (the length of the strings being longer than the length of an extended monkey hanging by his/her legs) (Plate 10). These behavioural components were not assumed to be novel for the tamarins (bipedal hanging, lifting and pulling being part of the behavioural repertoire of all the study animals) but the specific sequence of these necessary to succeed on the task (in its totality) was.

5.2.3 Design

The basic experimental design followed that of Thorndike (1898) in which a demonstrator animal performs a task in front of an observer, the test then being whether the

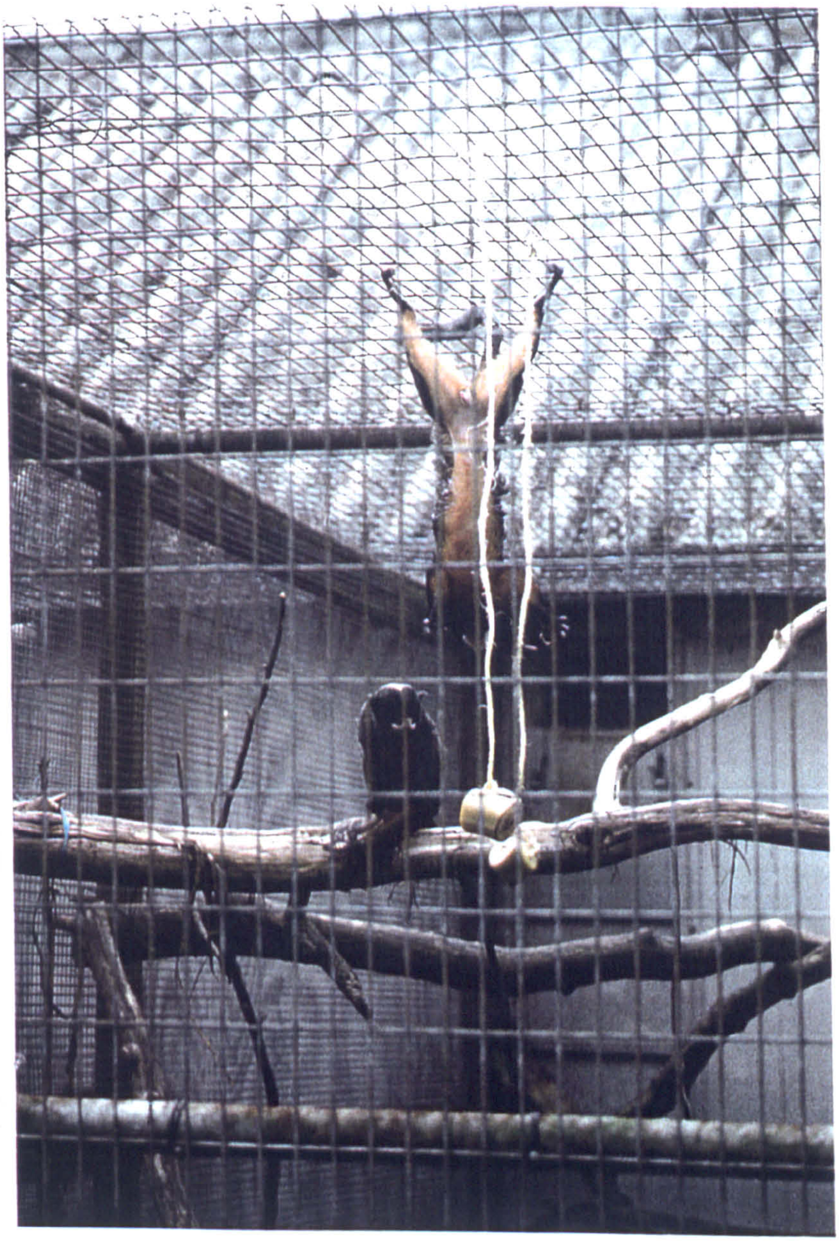


Plate 10: *S. labiatus* hanging from the mesh roof of the outdoor area of its enclosure in order to use the *grasping* strategy to obtain a piece of banana.

observer achieves some criterion of success on the task more quickly than when compared with a naïve animal who has not been allowed to observe a demonstrator.

The experiment was designed so that both species acted as demonstrators for their conspecifics and for their congeners, in order that comparisons can be made between intra-specific demonstrators and observers, and inter-specific demonstrators and observers. The experiment was designed in this way because it may be that one or both species learn from their congeners more quickly than they do from their own species, indicating an additional advantage to forming mixed-species troops over and above that due simply to an increase in troop size.

Such an experimental design also allows comparisons to be made between species in their rates of asocial learning (independent acquisition). If one of the demonstrator species learns the task solution, asocially, significantly more quickly than the other, say the *S. fuscicollis* do, than it might be that the *S. labiatus* benefit more from watching the *S. fuscicollis* than they would from observing their conspecifics. This too would constitute an additional advantage to forming mixed-species troops for *S. labiatus*.

For the intra-specific condition, three male-female pairs of *S. fuscicollis* performed as demonstrators for three male-female pairs of *S. fuscicollis*; and three male-female pairs of *S. labiatus* performed as demonstrators for three male-female pairs of *S. labiatus*. Intra-specific demonstrator and observer pairs were always related (usually parents and offspring) because it is inadvisable to house unfamiliar, unrelated individuals of the same species next to each other as, due to the fanatic territoriality of tamarins, they may fight viciously (Prescott, pers. obs.). The pairs were maintained as family troops and separated only for testing. To avoid age confounds, the number of pairs of parents or offspring acting as demonstrators and observers was counterbalanced.

For the inter-specific condition, three male-female pairs of *S. fuscicollis* performed as demonstrators for three male-female pairs of *S. labiatus*; and similarly, three male-female pairs of *S. labiatus* performed as demonstrators for three male-female pairs of *S. fuscicollis*. Interspecific demonstrator and observer pairs were normally maintained as mixed-species troops (and were therefore familiar with each other) and separated only for testing.

Testing was carried out between July and September, 1996, and between April and June, 1997. Species were tested in male-female pairs to minimise the stress of separation and more closely resemble the social foraging environment of the wild. However, this meant that, in both the intra- and inter-specific conditions, the second monkey of each male-female pair to complete the task had had the opportunity to observe its pair-mate. Consequently, only the data for the first monkey to complete the task were used in the analysis. This means, also, that the data are not confounded by the possible presence of '*scrounger*' individuals who simply exploit the skills of others (in this case, steal the food from the successful individual) without learning those skill themselves and as such block social learning and transmission (Giraldeau & Lefebvre, 1987; Fragaszy & Visalberghi, 1990; Beauchamp & Kacelnik, 1991).

5.2.4 Procedure

All tests were conducted before the tamarins' daily feed to ensure they were motivated to obtain the food reward. The experimental procedure was as follows:

(1) Two strings (50 cm in length) were suspended from the centre of the wire mesh roof of the outdoor portion of the enclosure of the male-female pair to be tested, and loaded with pieces of banana (2 cm in width), whilst the monkeys housed in all other cages were shut inside the indoor portions of their enclosures. This prevented the animals not yet tested from seeing the apparatus and the reaction of their neighbours to it. It also prevented those animals already tested from influencing the behaviour of those being tested, and minimised the possibility that study animals would spend time displaying to neighbouring troops. The pair acting as demonstrators were then allowed to exit the indoor portion of their enclosure, after which the connecting door between the indoor and outdoor portions of the enclosure was closed behind them. Recording started the moment the door was opened and continued for 30 minutes, or until both food items had been eaten, after which the strings were removed.

The pair were presented with the task in this way, once per day, until both individuals had been observed to succeed in obtaining the food at least twice. These animals were then considered to be 'trained demonstrators'. Data documenting their asocial learning of the task were termed 'naïve demonstrator data' and were later compared to that of observers.

(2) Subsequent, daily trials involved shutting out the second pair (those in the role of observer), into the outdoor portion of an adjacent enclosure and allowing them to

observe, through the mesh enclosure sides, the demonstrator-pair complete the task in a further three 30 minute trials. In each case, at least one of the demonstrators completed the task in each of the three trials.

(3) Immediately following the third observed successful trial, the observers were presented with the task themselves in the outdoor portion of their own enclosure, with the adjacently housed demonstrators (and all other troops) shut indoors (to prevent '*interference*' effects: see Zajonc, 1965; Zentall & Galef, 1988). The delay intervening between observing and having the opportunity to perform what was observed was minimised to maximise the motivation to perform on the task.

5.2.5 Recording Methods

Data were recorded directly onto a hand-held computer using THE OBSERVER 3.0 event recording computer-program (Noldus, 1993). The time at which each individual approached within and exited outwith 15 cm of the string, touched the string, and obtained the food item (made contact with hands or mouth) were recorded using all-occurrences sampling (Altmann, 1974). Any alternative ways in which the tamarins tried to obtain the food item (e.g., vertically clinging and leaping from one side of the enclosure to another, past the string), any calls and any competitive interactions (food stealing, agonistic behaviour and displacements: see Table 4.5) were also recorded *ad libitum*.

5.2.6 Data Analysis

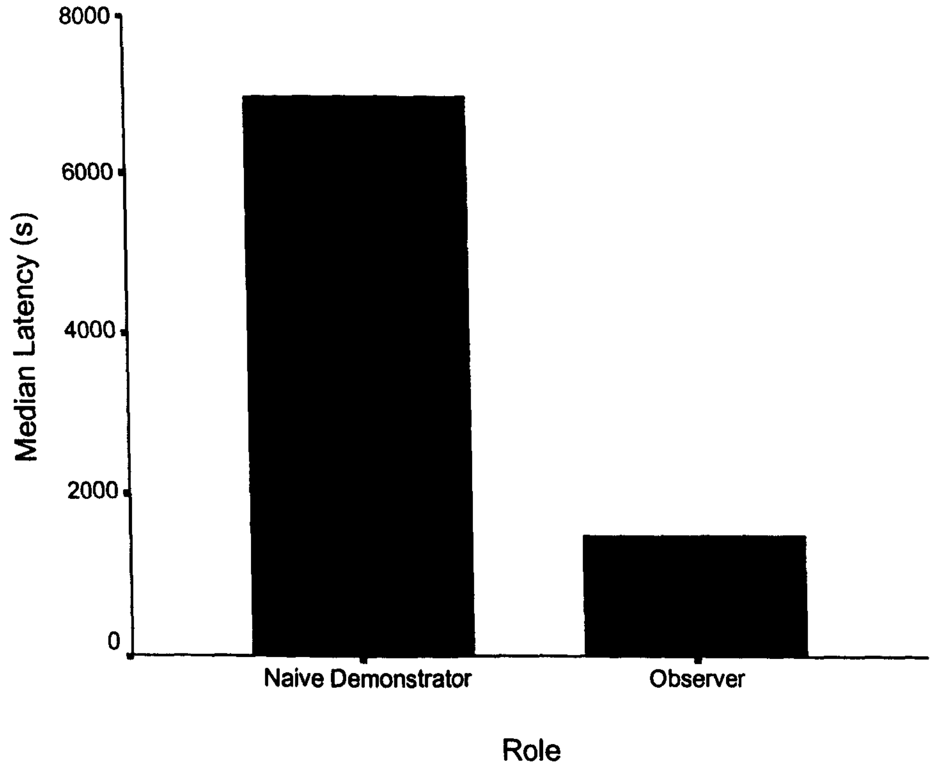
From the data collected, the latencies (in seconds) from exiting the indoor portion of the home enclosure to approach within 15 cm of the string, touch the string, and to obtain the food item, were determined for each individual in each trial. The latency for the first individual of each pair to obtain the food item on its first successful trial was added to the number of preceding unsuccessful 30 minute trials for that individual (since trials lasted for 30 minutes, after which the apparatus was removed if neither monkey had succeeded in obtaining the food item). This corrected 'true' latency was the used for analysis. 'True' latencies were similarly calculated for approaching within 15 cm of the apparatus and touching the apparatus.

Statistical comparisons between role (naïve demonstrator or observer), species, age or condition (intra-specific or intra-specific) were made using non-parametric Mann-Whitney U tests (with significance set at alpha < 0.05) because of sample-size limitations and deviations from normality. The Chi-square test was used to test for sex differences. Competitive interactions, calls and alternative ways in which the task was completed were so few as to not warrant statistical analysis.

5.3 Results

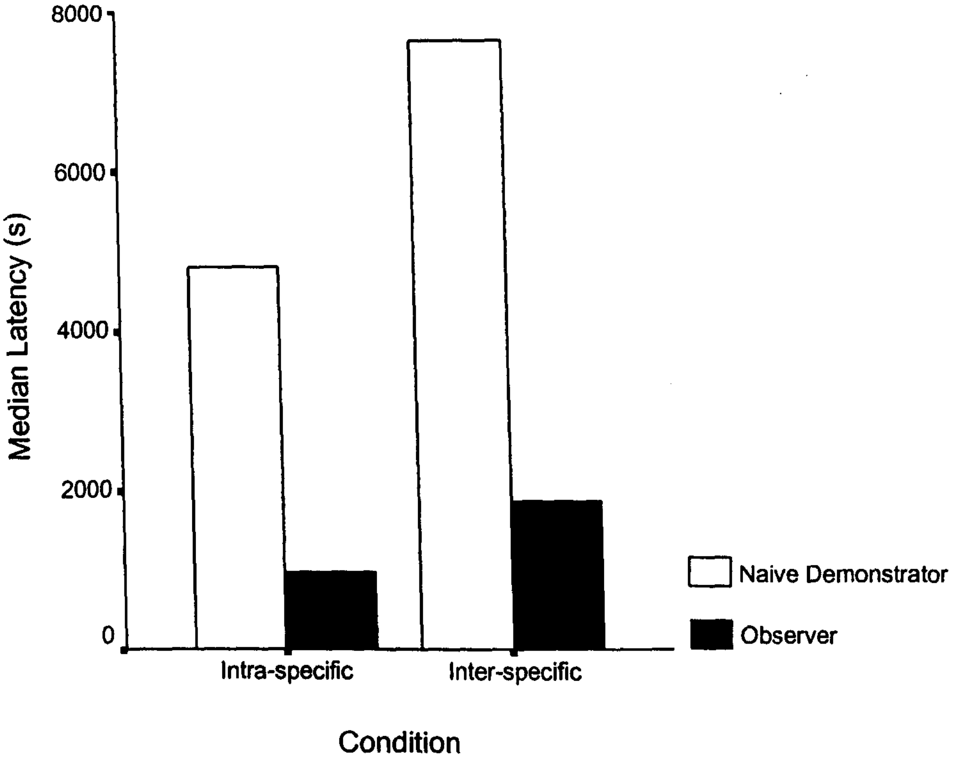
Overall (pooling both species intra- and inter-specifically), observers, which had had the opportunity to observe completion of the task by knowledgeable demonstrators of *either* species, successfully obtained the food item significantly faster than those that had not observed (the naïve demonstrators) ($z = -3.32$, $p < 0.01$; Figure 5.1).

Figure 5.1: Median latencies (seconds) to obtain food item for naïve demonstrators and observers, pooling species intra- and inter-specifically.



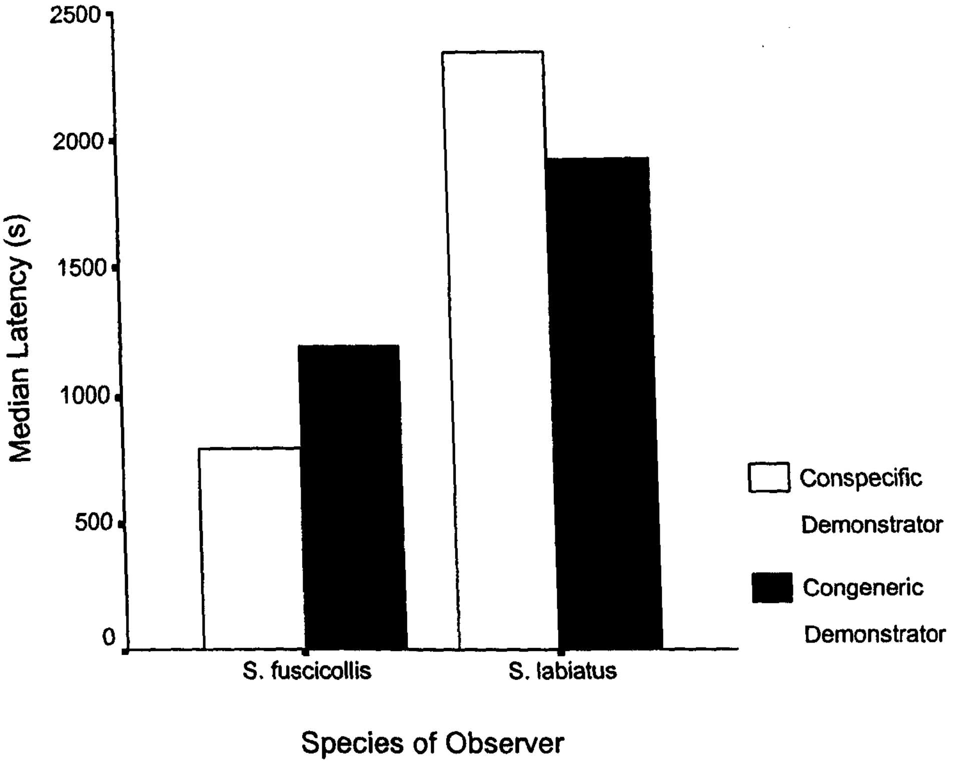
Collapsing across species, but splitting the data intra- and inter-specifically, it is found that, for both the intra- and inter-specific condition, observers were significantly faster to obtain the food item, than were their naïve conspecific and congeneric demonstrators ($z = -2.31$, $p < 0.05$, and $z = -2.02$, $p < 0.05$ respectively; Figure 5.2).

Figure 5.2: Median latencies (seconds) to obtain food item for intra-specific and inter-specific naïve demonstrators and observers.



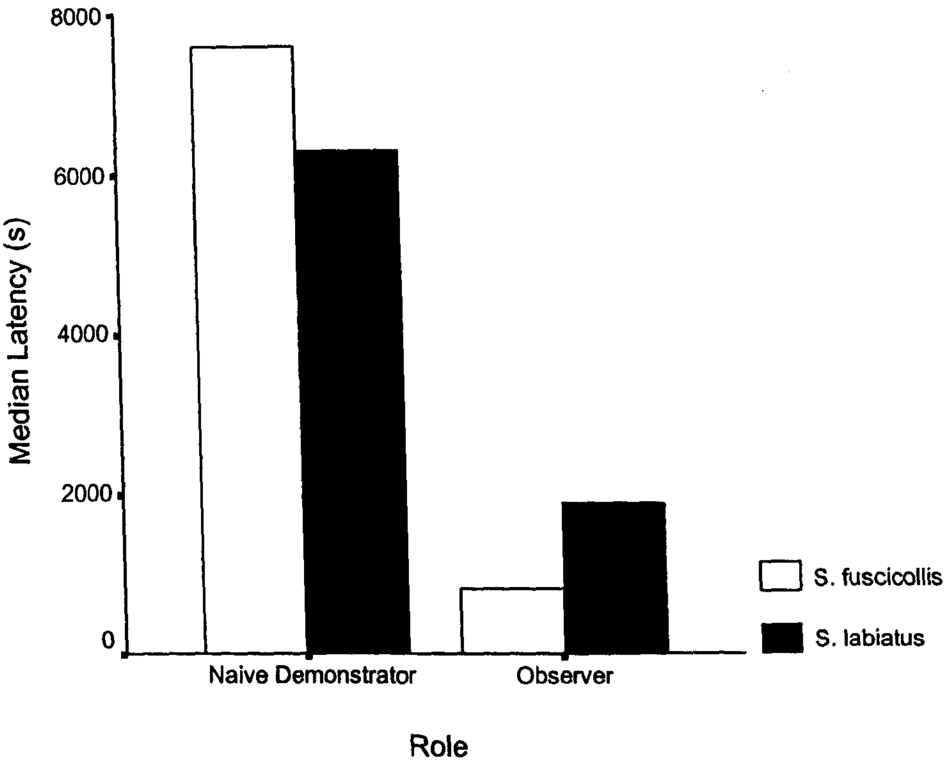
With regards to the significance of mixed-species troops, as described earlier, both species were tested both intra-specifically and inter-specifically to see if either may benefit from being in mixed-species troops because of the different propensities of the other species per se, or whether or not they might get equal or greater benefits from observing troop members of the same species discover and complete the food task. However, no significant effect for demonstrator species was found. That is, for both *S. fuscicollis* ($z = -0.96$, $p > 0.05$) and *S. labiatus* ($z = 0.00$, $p > 0.05$), the latencies to obtain the food item after observing conspecifc demonstrators did not differ from those after observing congeneric demonstrators. Neither was there a significant difference between the latency to obtain the food item by observer *S. fuscicollis* after having observed *S. labiatus* demonstrators compared with observer *S. labiatus* after having observed *S. fuscicollis* demonstrators ($z = -0.40$, $p > 0.05$; Figure 5.3).

Figure 5.3: Median latencies (seconds) to obtain food item for observer *S. fuscicollis* and *S. labiatus* after having observed conspecific or congeneric demonstrators.



Now, examining species differences in the rate of learning to complete the task, there was no significant difference between species in the rate of asocial learning by naïve demonstrators (z = - 0.12, p > 0.05), and, collapsed intra- and inter-specifically, there was no significant difference between species in the rate of social learning by observers (z = - 0.06, p > 0.05; Figure 5.4). So, in addition to the absence of an effect for demonstrator species, species did not differ in their rates of learning either as naïve demonstrators or observers.

Figure 5.4: Median latencies (seconds) to obtain food item for naïve demonstrator and observer *S. fuscicollis* and *S. labiatus*.



In order to reach a deeper understanding of what aspects of the demonstrator's performance may have influenced the acquisition of the technique necessary to reach the food item, a more detailed analysis of the behaviour and interactions during the acquisition period is needed. By examining the relations between the latencies to approach and touch the string, and to obtain the food item, we can identify exactly which of these behavioural components are facilitated by observation of a demonstrator. For example, it may be that the tamarins are facilitated merely to approach and touch the apparatus, and hence learn simply that it is non-threatening (in any case, such a reduction in neophobia may still be adaptive), rather than learning how to complete the task once in proximity to the apparatus. Indeed, the latencies to approach within 15 cm of the apparatus (Table 5.1) and to touch the apparatus (Table 5.2) all followed a similar pattern to the latencies to obtain the food item, with the exception of the lack of a significant difference in the latency to touch the apparatus for inter-specific naïve demonstrators and observers (Table 5.2). To examine whether the tamarins actually learnt how to complete the task, the following inter-behaviour latencies were calculated: (a) the latency to approach within 15 cm of the apparatus was subtracted from that taken to touch the apparatus to give the approach-touch latency; (b) the latency to approach the apparatus was subtracted from the latency to obtain the food item to give the approach-obtain latency; and (c) the latency to touch the apparatus was subtracted from the latency to obtain the food item to give the touch-obtain latency.

Table 5.1: Median latencies (seconds) to approach within 15 cm of apparatus

	Naïve Demonstrators	**Observers**	**Z value**
Pooling species intra- and inter-specifically	4507	767	z = -3.16, **p < 0.01**
Intra-specific condition	3844	945	z = -2.20, **p < 0.05**
Inter-specific condition	5570	567	z = -2.19, **p < 0.05**
	Conspecific demonstrators	Congeneric demonstrators	
S. fuscicollis observers	747	1301	z = - 0.48, p > 0.05
S. labiatus observers	945	251	z = - 0.64, p > 0.05
	S. fuscicollis	*S. labiatus*	
Naïve demonstrators	5145	4488	z = - 0.23, p > 0.05
Observers	915	573	z = - 0.20, p > 0.05
Observers from congeneric demonstrators	1301	251	z = - 0.58, p > 0.05

P-values refer to Mann-Whitney U test. Bold indicates a significant result.

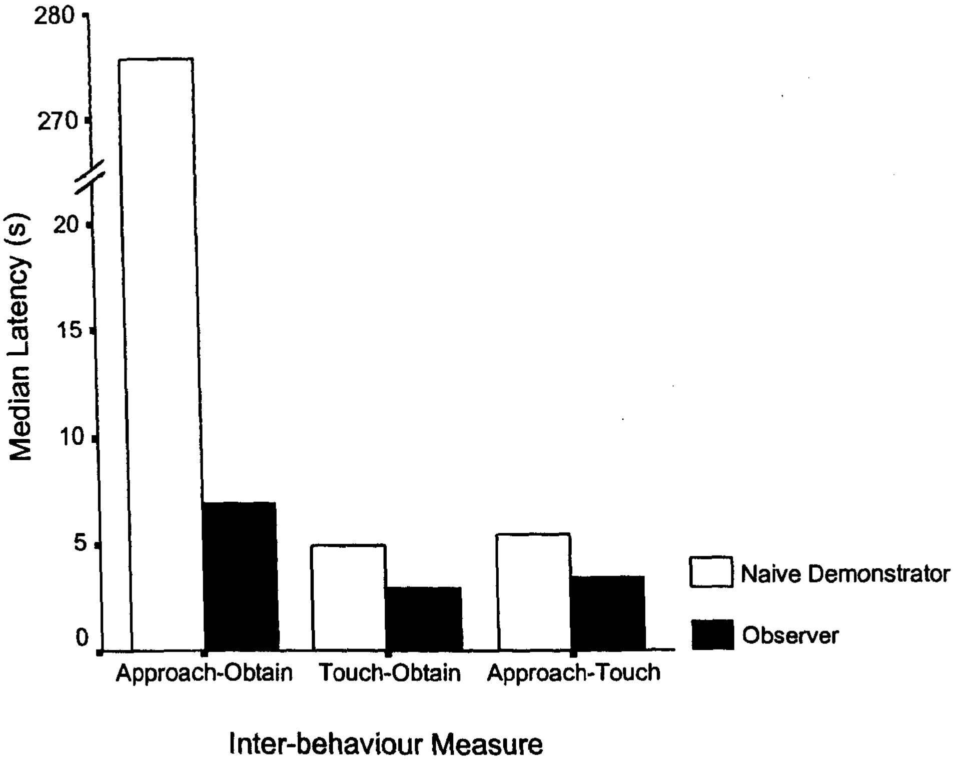
Table 5.2: Median latencies (seconds) to touch the apparatus

	Naïve Demonstrators	**Observers**	**Z value**
Pooling species intra- and inter-specifically	5368	769	z = - 3.26, **p < 0.01**
Intra-specific condition	4641	978	z = - 2.24, **p < 0.05**
Inter-specific condition	6009	623	z = - 1.96, p > 0.05
	Conspecific demonstrators	Congeneric demonstrators	
S. fuscicollis observers	752	1303	z = - 0.16, p > 0.05
S. labiatus observers	1021	361	z = - 0.16, p > 0.05
	S. fuscicollis	*S. labiatus*	
Naïve demonstrators	6026	4794	z = - 0.17, p > 0.05
Observers	917	684	z = - 0.29, p > 0.05
Observers from congeneric demonstrators	1303	361	z = - 0.40, p > 0.05

P-values refer to Mann-Whitney U test. Bold indicates a significant result.

It is found that, overall (pooling both species intra- and inter-specifically), observers are facilitated to obtain the food item having approached the apparatus (z = - 2.26, p < 0.05) and once having touched the apparatus (z = - 2.33, p < 0.05). Latency to touch the apparatus after approaching it is not facilitated by observation (z = - 1.74, p > 0.05; Figure 5.5).

Figure 5.5: Median inter-behaviour latencies (seconds) for naïve demonstrators and observers, pooling intra- and inter-specifically.



There were no significant sex affects. Pooling both species intra- and inter-specifically, male demonstrators were just as likely as female demonstrators, and male observers were just as likely as female observers, to be the first of each pair to approach within 15 cm of the apparatus, touch the apparatus, and obtain the food item (Table 5.3).

Table 5.3: χ^2 values for sex differences in the frequency to be the first to perform the three behaviours by naïve demonstrators and observers (pooling species intra- and inter-specifically).

Role	**Behaviour**	**χ^2 value**
Naïve demonstrators	Approach within the apparatus	$\chi^2 = 0.33$, df = 1, $p > 0.05$
	Touch the apparatus	$\chi^2 = 0.00$, df = 1, $p > 0.05$
	Obtain the food item	$\chi^2 = 0.00$, df = 1, $p > 0.05$
Observers	Approach within the apparatus	$\chi^2 = 0.33$, df = 1, $p > 0.05$
	Touch the apparatus	$\chi^2 = 0.33$, df = 1, $p > 0.05$
	Obtain the food item	$\chi^2 = 1.33$, df = 1, $p > 0.05$

Nor were there any significant age effects. In the intra-specific condition (pooling species), non-adults (juveniles and sub-adults: see Section 4.4) were just as quick as adults to learn the task (approach the apparatus, touch the apparatus, and obtain the food item) asocially (i.e., as demonstrators) ($z = -1.964$, $p > 0.05$), and socially (i.e., as observers) ($z = -0.926$, $p > 0.05$). Furthermore, non-adults observing adults were no quicker than adults observing non-adults ($z = -1.964$, $p > 0.05$).

5.4 Discussion

The aim of this experiment was to investigate whether observation of an experienced conspecific or congener has any influence on the rate at which an individual tamarin learns how to access food in a novel foraging task. The opportunity to observe an experienced individual clearly did lead to faster successful completion of the task than did independent, asocial learning. Such a facilitatory effect may have considerable adaptive value in wild tamarin troops, in that individuals can benefit by learning about novel or changing aspects of their environment more quickly through observation of experienced troop members than by asocial learning. Tamarins inhabit tropical rain forests. These are generally characterised by high species diversity but low species density (Milton, 1988) and thus it is probable that foraging individuals will come across potentially exploitable but novel food resources. In addition, each new generation is likely to come into contact with foods not previously encountered. If learning how to exploit these resources can be facilitated by observation, then social learning will be an adaptive strategy in enabling the rapid, effective and safe exploitation of these novel food resources, possibly at reduced energy cost and predation risk. Rapid exploitation of fruit resources requiring the grasping strategy may be important for tamarins as they are especially vulnerable on the thin, terminal branches of tree crowns, particularly to their main predators, raptors (Peres, 1993a). Provided species can learn from each other, association, through an increase in troop size, would increase the opportunity for information transfer between individuals accordingly.

Social learning about food may be particularly important for the younger members of the troop who, in their naïve immaturity, face a host of new food-related challenges for which the need to rapidly acquire the necessary behavioural solutions may be particularly acute (Galef, 1976). In fact, the whole feeding culture of the troop, the palatable species of plants and animals, their location and their methods of acquisition and processing may have to be learnt during adolescence. One might expect naïve juveniles to learn faster than naïve adults, then. However, no effect of age was found in this experiment. There was also no effect for sex. This is in contrast to Box (1997) who observed sex differences for *S. fuscicollis* and *S. labiatus* on an unfamiliar foraging task (extraction of embedded food from perspex boxes). Adult females attempted the task more frequently than males, spent longer periods attempting to obtain the food, and removed food from the boxes more often.

With regards to the adaptivity of *mixed-species* troops per se, neither species showed a significant difference in their latency to complete the task after having observed a conspecific demonstrator as opposed to a congeneric demonstrator. This is perhaps surprising given that, in all mixed-species troops studied to date, inter-specific social interactions are rare in comparison to intra-specific ones (Pook & Pook, 1982, for *S. fuscicollis* and *S. labiatus*; Norconk, 1986; Heymann, 1990a, for *S. fuscicollis* and *S. mystax*). Those inter-specific interactions that do occur are most often agonistic and associated with exploitation of monopolisable plant food resources. This lack of an effect for demonstrator species may simply be an indication of the considerable cohesion, integration and tolerance of tamarin mixed-species troops in the wild and in captivity. It is reported that more affiliative inter-specific interactions occur in captivity than in the wild (e.g., grooming and social play: Heymann & Sicchar-Valdez, 1988; Heymann *et al.*, 1996; Hardie, 1997). Certainly both species of observers in this study spent brief but frequent periods of time intently observing their demonstrators behaviour at the apparatus, regardless of their species, and anecdotally, there appeared no restriction on the general behavioural repertoire of either species as a result of the inequality in dominance between them.

Being able to learn form congeners as well as conspecifics may lead to an additional advantage for mixed-species troops over single-species troops, in that individuals can benefit from an increased knowledge base (i.e., the species-specific experience of their own species and that of their congeners). This possibility is important for tamarins given that, in all mixed-species troops studied thus far, there is vertical segregation between the associating species (with *S. fuscicollis* occupying a lower height in the forest than their congeners: Yoneda, 1981; Pook & Pook, 1982; Terborgh, 1983; Norconk, 1986; Buchanan-Smith, 1990a) and thus the potential for differential knowledge regarding separate forest strata. In this experiment, in addition to the absence of an effect for demonstrator species, there were no differences between species in their rates of learning, either as naïve demonstrators or observers. Thus it cannot be concluded that mixed-species troops confer any additional advantage above that which would be accrued in monospecific troops of the same size. In any case, large monospecific troops may be unattainable due to feeding competition and intra-sexual conflict between reproductive competitors (Buchanan-Smith & Hardie, 1997). Moreover, since there were no differences between the species in their rates of learning, and since *S. labiatus* having observed *S. fuscicollis* were no faster to complete the task than were *S. fuscicollis* after having observed *S. labiatus*, the advantage accrued to each species from observing appears symmetrical.

Although I wished to concentrate upon the adaptive function of the monkeys' learning, in the context of mixed-species association, rather than the means by which it was achieved, it is possible to speculate upon the mechanism at work. Identification of a mechanism is important in order to further our understanding of comparative primate intelligence. We are faced with the difficult task of sorting out a variety of processes occurring in social situations which can influence an observer's behaviour and lead to similar behaviours in the observer and observed. Our problem is thus one of exclusion of alternative mechanisms, an especially difficult problem given that there is no uniformly accepted classification of social learning mechanisms at present (e.g., Galef, 1988; Whiten & Ham, 1992; Heyes, 1993, 1994).

Since the observers did not have the opportunity to interact with the stimulus at the same time as the demonstrators, we can discard *social facilitation* (i.e., an indiscriminate increase in general activity as a result of observation: Zajonc, 1965) as a potential explanation for their matching behaviour and instead infer that some long-term behavioural change had occurred in the observers. Furthermore, in separating the demonstrator's apparatus from that of the observer by the use of duplicate cages we controlled for *local enhancement*, whereby the demonstrator's behaviour increases the probability that the observer will attend to the locale with which the demonstrator interacted (Thorpe, 1963). Instead, we need be concerned with four types of social learning, namely *stimulus* *enhancement* (Spence, 1937), *imitation* (Thorndike, 1898; Morgan, 1900), *goal emulation* (Tomasello, 1990; Whiten & Ham, 1992), and *response facilitation* (Byrne, 1994).

For our purposes, *stimulus enhancement* refers to the demonstrator's behaviour increasing the probability that the observer will attend to/interact with stimuli of the same physical type as those with which the demonstrator interacted. *Imitation* refers to cases in which, as a result of observation, the observer copies the form of a novel behaviour from the repertoire of the demonstrator. *Goal emulation* refers to the observer duplicating the results of the demonstrators behaviour (the goal) but not its methods. *Response facilitation* refers to the increased probability of the observer performing a particular behaviour (already in its repertoire) as a result of observing the demonstrator performing the same behaviour.

Since observers were facilitated to approach the apparatus, and to touch it once in proximity to it, one mechanism at work here appears to be stimulus enhancement. The observer may have completed the task by simple trial and error learning but learnt from the demonstrator to direct its appetitive actions towards the apparatus. However, since the categories of social learning are not mutually exclusive it is possible, in principle, that the demonstrator played several roles simultaneously. Thus, the possibility remains that, through its behaviour at the string, the demonstrator increased the probability that the observer would interact with the apparatus (stimulus enhancement), and furthermore, may have acted as a model regarding the actions necessary to obtain the food item (imitation). Unfortunately, in recording simply the latency to perform the various behavioural components necessary to succeed on the task, we are ill-prepared to confirm the presence of imitation. As described by Whiten and Ham (1992) for the observer-demonstrator paradigm used here,

> *"while speed of learning can be easily and objectively measured, it is insufficient to discriminate between stimulus enhancement and imitation"* (p. 242).

In order to distinguish explicitly between these two categories of social learning, one must use a '*two-action method*' (Dawson & Foss, 1965), where there are two possible ways in which to complete the experimental task and one looks to see if the observers tend to complete the task using the method which their demonstrators used in preference to the alternative method. Using this technique, Bugnyar and Huber (1997) have found *C. jacchus* able to imitate their conspecifics either pushing or pulling a pendulum door to open a wooden box (or at least '*mimick*', excluding insight or any perception or understanding of how the copied behaviour is designed to bring about the goal: after Tomasello, 1996). The task we are concerned with here could be completed successfully in one way only and so cannot provide evidence for imitation. Furthermore, because of the paucity of data on differences in action pattern (the tamarins were not really observed to use alternative strategies to achieve the goal: the food item), we are also unable to provide evidence for goal emulation.

With regard to our remaining mechanism, response facilitation, it is interesting to note that, although observers were facilitated to touch the string, they were also facilitated to complete the task once having done so. This suggests that they learned something about the actions necessary to succeed on the task and obtain the food item, apart from any intrinsic orienteering to the stimulus. So, in addition to having their attention and subsequent manipulations directed to the apparatus, the observers were also selectively enhanced to apply particular matching behaviours already in their repertoire (response facilitation) to solve the problem rapidly. Byrne (1995) writes that such a combination of stimulus enhancement and response facilitation is a powerful one, quite apart from the possibility of goal emulation.

We appear, then, to have an ecologically orientated example of stimulus enhancement and response facilitation in two species of tamarin. Increased speed of learning on the task by observers results from facilitation of the observer by the demonstrator into a stimulus situation to which the observer is predisposed, as a result of observation of the demonstrator and of previous experience, to respond in a certain way as to acquire the food item. Hence, the matching of behaviour with that of the demonstrator. It has been suggested that, in many cases of natural social learning, successful transmission of information depends upon the pre-existence of certain relevant experiences, or responses that occur in the natural context of the monkey's behaviour, being simply reinforced through interaction (Hauser, 1988).

In past experiments, captive monkeys have often failed to show forms of social learning such as these (see Whiten & Ham, 1992). The slow rate of learning described in previous studies may reflect irrelevance of the testing environment to the monkeys' natural habitat, pronounced hierarchical differences among dyads, or may be a result of traditional fixed-trial procedures which allow only limited periods of interaction between individuals. In the field, where animals have the freedom to interact continuously, learning processes may be much more rapid (Galef, 1976). Reports of rapid learning for objects associated with food do exist for tamarins in captivity however. Hardie (1995) found troops of *S.*

fuscicollis and *S. labiatus* to respond differently to objects that had been paired with food and those that had not after a single trial. Furthermore, this information could be retained for a period of at least 7 weeks and could be transferred between the species. Similar swift learning was again demonstrated in an eight-member family of *S. fuscicollis* (Menzel & Juno, 1982, 1984) who, on a single exposure to objects associated with food, increased their frequency of approach to those objects on the next trial. Such rapid learning in tamarins may reflect species-specific propensities for particular kinds of learning or learning capacity (i.e., adaptive specialisations: Rozin & Kalat, 1971) in relation to the distribution pattern of major food resources (Menzel & Juno, 1985; Milton, 1981, 1988), or to social structure (Goodall, 1973; Itani & Nishimura, 1973; Cambefort, 1981) and social dynamics (Coussi-Korbel & Fragaszy, 1995). For example, Menzel and Juno (1985) found *S. fuscicollis* to exhibit exceptionally rapid learning of, and an ability to remember from one day to the next, the visual appearances and relative positions of many food-associated objects simultaneously. This, they suggest, is related to the concentration in space and time of the monkeys' primary fruit resources in the wild: fruits that occur in tiny, scattered incremental units and that, furthermore, ripen in a piecemeal fashion. With regards to learning and social dymanics, Coussi-Korbel and Fragaszy (1995) suggest that *Saimiri* (squirrel monkeys) would be less likely than tamarins to acquire information from one-another about the non-social environment because, owing to competing attentional demands arising from a modest hierarchical organisation (in captivity at least), they are less likely to focus their attention upon one-another for more than brief moments. It is interesting to note in this regard that, in a study by Boinski and Fragasy (1989), juvenile *S. oerstedi* (red-backed squirrel monkey) were observed to go through a painful process of trial and error learning to rub noxious spines of caterpillars before eating them, even though they had seen adults rubbing them off safely with their tails on numerous occasions. In this study, during the phase in which the observers could observe demonstrators, both spent reasonably brief but frequent periods of time observing one-another. This brings us back to the proposition discussed in Chapter 3: that the transmission of information through ongoing behaviour will be greater in species exhibiting a high degree of tolerance and co-ordination in time and space. These are characteristics of both single- and mixed-species tamarin troops.

5.5 Conclusion

Tamarins spend a great deal of their time foraging for food, the identification and acquisition of which is likely to constitute one of their greatest environmental challenges. It would appear that foraging in a cohesive troop can support learning of the method of acquisition of food from other troop members; the social interaction with others increasing the opportunities for an individual to encounter the appropriate environmental stimuli for learning to occur and/or providing models of the behaviours required to acquire the food. Moreover, since individual tamarins are able to learn from their congeners as well as their conspecifics, mixed-species troop formation, by increasing troop size, can facilitate the transfer of such information, and furthermore, may lead to an additional advantage over similarly-sized single-species troops in that individuals of both species may be able to benefit from the species-specific knowledge of their own species and that of their congeners.

Chapter 6

Social Learning About Food Palatability

"Monkeys feeding in a tree that is only just coming into fruit are as selective in choosing what they will eat as any good housewife in a market, inspecting each fruit closely and lifting it up to their nostrils for a quick sniff before risking a bite."

[Attenborough, 1995: p. 25]

6.1 Introduction

That the natural history of tamarins may have a profound effect on their susceptibility to social influence was discussed in Chapter 3. It was suggested that, given such high levels of co-operation and cohesion within and between associating tamarin species, one might expect that social learning could play an important role in how these monkeys respond to food-related challenges in both single- and mixed-species troops. Selecting a nutritionally adequate diet from the range of ingestible substances available, together with avoiding foods that are valueless or dangerous to eat, is just one of the food-related challenges all animals face in their natural environment. To survive to reproduce, they must choose foods that provide all the nutrients necessary for self-maintenance and reproduction and avoid eating lethal amounts of toxic foods. One might expect that the opportunistic, generalist tamarins, feeding as they do on a wide variety of food parts or species, will often have to deal with unpalatable food items (e.g., unripe fruits, poisonous plants or insect prey) and that considerable selective pressure may operate to favour transmission of information concerning the safety of such potential food items between troop members. Although they take small vertebrates, plant exudates and nectar, the majority of the tamarin diet consists of ripe fruit and insect prey. Let us explore in more detail, then, whether selecting safe, nutritious, palatable fruit and insect prey is likely to be a significant problem for tamarins.

Field studies indicate that insects account for some 30 - 77 % of the total feeding and foraging time of tamarins and that tamarins are highly selective in their choice of insect prey (Garber, 1980, 1988b; Terborgh, 1983; Snowdon & Soini, 1988). As described in the previous chapter, different genera, species or developmental stages of this insect prey may possess considerable physical and chemical defences, the latter often indicated by conspicuous aposematic colouration. It is likely that the selectivity observed for tamarins feeding on insects reflects foraging decisions made on the basis of their experience of the nutritional value and defensive capabilities of such prey.

Ripe fruits account for 20 - 65 % of total feeding and foraging time in all tamarin species studied (Garber, 1993a) and tamarins are thought to constitute an important group of dispersers for rain forest plant species (Terborgh, 1983; Garber, 1986; Knogge *et al.*, 1998). Although few observers of primates have collected systematic data on feeding on fruit at different stages of ripeness (probably because of the difficulty in distinguishing developmental changes not indicated by changes in colour), primates are known to be highly selective about the stage of ripeness of their fruit (Chivers, 1977; Waser, 1977). Before a fruit ripens it may taste very unpleasant indeed. This is because, from the time of fruit set until the mature fruit is presented to the dispersal agent, the developing seed/s is/are very susceptible to predation, making the immature fruit the primary defence of the plant against herbivorous animals. The whole dispersal strategy of the plant would be spoiled if the dispersal agent ate the fruit before the seeds it contained were properly developed. So, whilst development of the seeds is in progress, the sap in the fruit flesh is so acid and sour that it tastes very unpleasant. In addition, it may contain high levels of toxic secondary plant compounds (SPCs) (e.g., alkaloids) and/or digestion inhibitors (e.g., tannins, lignin) such that any animal that eats the fruit is likely to become quite ill. In this way, the plant dissuades herbivorous animals from predating upon its seeds. As the seeds develop, the level of potentially harmful substances in the fruit flesh decreases whilst the concentration of palatable simple sugars increases (often just as the seed is completed, such that the change from ripe to unripe is very rapid: e.g., Coombe, 1976; Ho, 1992).

Once ripe and delectably sweet, however, primates face another problem, in that the fruit is likely to be eaten by one of the many fruit eaters in the rain forest. Consequently, the best strategy for any primate may be to select fruit that is barely ripe (Diamond, 1978), but this presents a tracking problem in that they can select nutritionally valuable, non-toxic foods only insofar as those qualities are reflected in chemical or physical cues that they can detect. Although changes in smell, colour and texture are often associated with ripening and may represent key attributes for determining eating quality, not all fruits demonstrate changes in these cues during ripening, and given that intense inter-specific competition between frugivores may encourage hasty consumption, there is a real possibility that frugivorous primates may make mistakes and that these may sometimes be costly. Moreover, in all New World monkeys studied thus far with the exception of *Alouatta* (howler monkeys), males are dichromatic in their colour vision whereas females are either dichromatic or trichromatic (Mollon *et al.*, 1984; Jacobs *et al.*, 1996). Given that the potential major advantage of trichromacy seems to be the detection and identification of food, particularly ripe fruit in the dappled light of leaves (Polyak, 1957; Mollon, 1989, 1991; Osorio & Vorobyev, 1996; Regan *et al.*, 1996), and that trichromacy is considered necessary for the efficient detection and selection of particularly yellow and orange fruits amongst foliage (the colour of fruits specialised for attracting monkeys: Janson, 1983; Gautier-Hion *et al.*, 1985; Julliot, 1996), dichromacy may have an adverse impact on the ability of some individuals to use colour to detect and select ripe fruits (Buchanan-Smith *et al.*, unpubl. MS).

Changes in the nutrient and SPC content of fruit may also occur as a result of insect damage or infestation, rendering the fruit unpalatable. This is not an insignificant problem. In the fruit crop of *Cassia grandis* (Leguminosae), for example, as much as 75% of the small green pods may be attacked by lepidopteran larvae during the first six months of the crop's life (Edwards & Wratten, 1980). Although the additional protein might be a welcome benefit to some frugivorous primates (depending upon the predator and prey species), the toxic compounds that the insects themselves may possess, or that the plant may produce in response to its insect attackers, most certainly would not be. They would do well to look for signs of damage (e.g., small holes, discolouration) indicating infestation and to avoid such fruit. Evidence that fruit infestation reduces the probability of consumption in primates has been documented in *Alouatta seniculus* (red howler monkey) (Julliot, 1996).

Given these problems in selecting nutritionally valuable, non-toxic food items, one would expect considerable selective pressure to operate upon tamarins to learn about the palatability and toxicity of their food, and the significance of any cues indicating these. Although the precise mechanisms by which individual primates acquire such information are not well known, it is likely to be through individual learning processes such as trial and error and one-trial taste aversion learning (Jouventin *et al.*, 1976; Whitehead, 1981).

However, if, in addition to individual, socially-independent (asocial) learning, individuals can learn from one another about the value and characteristics of poor, dangerous or novel foods (or if they can respond to the aversive behaviour of others at the particular instance in time that those others are consuming such foods) they may save themselves from energetically costly mistakes or sampling and be able to expand their diet more safely.

Unfortunately, in primates, the acquisition and social transmission of food preferences and food avoidance has been less well studied than other aspects of foraging behaviour (Visalberghi, 1994). However, it has long been suggested that, for young primates, both are strongly influenced by the activities and choices of their mother and the other troop members in general (e.g., Kawamura, 1959; Hall, 1963; Goodall, 1986). Empirical evidence for the acquisition of food preference from conspecifics comes from Whitehead (1986), who observed that infant *A. palliata* (mantled howler monkey) attended to their mothers during leaf feeding and ate leaves from only those species that she and other troop members fed upon, usually after them. This led Whitehead to propose that learning which species of leaves are safe to eat is a socially dependent process for this species. Ingestion of fruit, however, appeared to be less influenced by social context and was therefore assumed to be relatively unconstrained by social learning. Whitehead concluded that the two classes of food have served as selective forces governing the evolution of two separate learning mechanisms. Presumably, natural selection has favoured learning from others about which types of leaves to feed upon, but not which types of fruits, because leaves typically contain greater quantities of noxious substances than do fruits.

Evidence that the presence of conspecifics can enhance the inclusion of a novel palatable food item into the adult diet has been provided by Visalberghi and Fragaszy

(1995) for *C. apella*, Hikami *et al.* (1990) for *Macaca fuscata* (Japanese macaque), and Watts (1985) for *Gorilla gorilla beringei* (mountain gorilla). Visalberghi and Fragaszy (1995) suggest that the most important effect of this social facilitation towards novel foods is not on consumption at the first encounter (i.e., learning that the food is safe to eat), but on its longer term consequences for repeated sampling of the novel food (i.e., its eventual inclusion into the diet). In a later study, Visalberghi *et al.* (1998) found that captive *C. apella* treated unfamiliar foods as familiar after as little as five successive encounters. The authors concur with the studies of Hikami *et al.* (1990) and Watts (1985) in concluding that enhancement of the consumption of novel foods under social conditions is adaptive in providing a means of expanding the diet safely.

Social facilitation of the consumption of novel food on first encounter has also been observed in callitrichines (Vitale & Queyras, 1997). Compared to their behaviour when alone, naïve juvenile (5 - 6 months old) *C. jacchus* were facilitated to consume novel foods in the presence of their older (11 months - 5 years), experienced troop mates (although the juveniles did respond quickly to novel foods when alone without the need to observe or interact with their troop mates). That the majority of troop members, not just the mother, will have a pervasive effect on the feeding preferences of youngsters is particularly likely in callitrichines given that, in addition to a social organisation characterised by a high degree of within family cohesion and co-operation (see Section 3.4), they rear their offspring communally. Usually only one female breeds and all members of the troop, including parents, older siblings and sometimes unrelated animals, help carry, groom and share food with the infants (see Section 1.2.3). This helps shift the cost of infant care from the mother to other troop members, enabling her to quickly re-direct some of her reproductive investment towards her next litter (Garber & Leigh, 1997). In fact, the

Callitrichinae are considered unique amongst non-human primates in the extent to which they voluntary share food with infants (Feistner & McGrew, 1989; Feistner & Price, 1991), and such extra-maternal provisioning is a critical supplement to the diet of the infants who may be continue to be provisioned until 7 - 9 months of age (Goldizen, 1987b; Snowdon & Soini, 1988). In most cases, the sharing is initiated by the infant (*begging*), who approaches the possessor of the food item and tries to take it from him/her, using hands or mouth, often whilst vocalising. In *L. rosalia* and *S. oedipus*, however, food *offering* has been observed also, whereby the possessor of the food item initiates the sharing by adopting a specialised posture and giving a characteristic 'food call' to attract the infant, who then approaches to take the food (Brown & Mack, 1978; Feistner & Chamove, 1986; Feistner & Price, 1990). Offering is thought not to occur in *S. fuscicollis* (Moody & Menzel, 1976, pers. obs.) or *S. labiatus* (Coates & Poole, 1983, pers. obs.).

Food sharing would appear to be an excellent way for infants and juveniles to learn about the palatability and nutrient quality of food items from other troop members, thereby avoiding experimentation with potentially harmful food stuffs. However, in an experiment with *L. rosalia*, Price and Feistner (1993) found no evidence that adults actively taught infants an appropriate diet through food sharing, or that infants learnt about novel food items by first obtaining them from older troop members. Instead they found that adults, rather than adjusting their behaviour to impart information on novel foods to infants, adjust their behaviour to ensure that infants receive adequate amounts of foods that are rare or difficult for the infants to obtain themselves because they lack the necessary physical strength or dexterity (i.e., these are the characteristics of the food items shared with infants). Similar findings have been made for *P. troglodytes* where passive food transfer from mother to infant is common during the first and second years of life and is biased towards items difficult for the infant to acquire or process itself (Assersohn & Whiten, 1998). Food sharing in tamarins is surely biologically significant but, on the strength of the evidence provided by Price and Feistner, does not help infants learn from experienced individuals about the palatability and edibility of novel food. Nevertheless, the possibility still remains that infant tamarins do learn about diet by observing the feeding behaviour of adults and other troop members.

It appears that, with the possible exception of *P. troglodytes*, which has been observed to demonstrate behaviours preventing the consumption of novel food by another individual (e.g., Nishida *et al.*, 1983), active teaching is not involved in learning an appropriate diet in non-human primates. Nor, is there evidence, or at least there is very little, that monkeys learn to avoid noxious foods from the food avoidance behaviour of others (Fairbanks, 1975, for *Macaca nemestrina* (pig-tailed macaque) and *Ateles geoffroyi* (black-handed spider monkey); Jouventin *et al.*, 1976, for *Mandrillus sphinx* (mandrill); Cambefort, 1981, for *P. ursinus* and *Cercopithecus aethiops* (vervet monkey); Hikami, 1991, for *M. fuscata*). In all these studies, knowledgeable individuals did nothing to prevent naïve individuals from eating noxious food, nor did the knowledgeable individuals avoidance of the food result in the naïve individuals avoiding the food also. This is perhaps unsurprising since, intuitively, it is more difficult to learn from the absence of behaviour in others (the fact that a food is left untouched) than it is from its presence. Individuals would presumably need to observe both consumption of the noxious food and the subsequent ill-effects on the consumer within a reasonably brief period of time in order to form a causal association between the two (if indeed they are able). Rather, what appears to happen is that, if individuals have learned that a certain food is noxious, and they spend time feeding with other individuals that are eating that food, then their own aversion is diminished: they will eat the food again. For example, in a study by Hikami *et al.* (1990), infant *M. fuscata* were aversively conditioned to two new foods, whereas their mothers were aversively conditioned to only one of the two foods. Mother-infant pairs were then watched during repeated co-feeding sessions, where it was observed that the infants started to eat the food their mother consumed and continued to avoid the food avoided by both the mother and the infant. Queyras and Vitale (pers. comm.) have observed social interaction with non-averse individuals to promote extinction of an aversion to a target food in *C. jacchus*, and similar findings have been made with *Rattus norvegicus* (Norway rat) (Galef, 1986), *Crocuta crocuta* (spotted hyena) (Yoerg, 1991) and in ornithological studies (Alcock, 1969; Turner, 1964).

Overcoming existing aversions to foods, following a change in ecological conditions (e.g., fruit ripening), may be as important as learning the aversions in the first instance. An ability to rapidly adapt to changes in the palatability of food resources may have considerable adaptive value in reducing inter-specific competition by increasing the range of food items within which a species can switch following ecological change. Social learning may be important in enabling a more rapid and uniform response to such changes. In fact, foraging individuals (particularly generalist ones) ought to balance caution towards potentially harmful food-stuffs with an inclination to sample familiar, and unfamiliar foods in small amounts, before deciding that they are safe.

Following the work of Hikami *et al.* (1990) and Queyras and Vitale (pers. comm), I wished to examine whether social interaction with non-averse individuals would promote the extinction of food avoidance in tamarins and, in addition, whether extinction could result from inter-specific interaction as well as intra-specific interaction. As demonstrated in the previous chapter, social learning about food need not be confined to learning from members of one's own species. Given that dietary overlap for fruit is high between *S. fuscicollis* and *S. labiatus* (Yoneda, 1984a; Buchanan-Smith, 1990a; Hardie, 1998), if they can learn about fruit palatability from congeners as well as conspecifics, then this may constitute an advantage to forming mixed-species troops in that they can benefit from the increased number of individuals in a mixed-species troop and the (perhaps divergent) experience of congeneric troop members. In addition to any bearing on the function of mixed-species tamarin troops, given the paucity of data on social influences on food choice in primates, such an experiment is important generally in understanding how animals consume an appropriate, nutritionally adequate diet. The two experiments that follow, Experiments 2 and 3, are concerned with intra-specific and inter-specific social influence on food aversion, respectively. An adult and a juvenile male-female pair of the same species (Experiment 2), or an adult male-female pair of *S. fuscicollis* and one of *S. labiatus* (Experiment 3), were presented with two foods, one of which was considered distasteful by one of the pairs, the other palatable, and their behaviour compared pre-interaction, during interaction, and post-interaction to see if an established food preference would be altered following interaction as a result of social learning.

6.2 Experiment 2: Intra-Specific Social Enhancement of the Extinction of a Food Aversion

The aim of the experiment was to investigate whether a spontaneous preference for a particular food shown by a pair of one species could influence an induced aversion to that same food in a pair of conspecifics.

6.2.1 Study Animals

The study animals were four adult and four juvenile male-female pairs taken from two troops of *S. fuscicollis* (SF6, SF10: Table 4.3) and two of *S. labiatus* (SL4, SL6: Table 4.4) housed in separate indoor-outdoor enclosures in the 'Old Marmoset-House'. Further details of housing and husbandry are given in Chapter 4 (Section 4.6).

Unfortunately, due to the extreme aggression tamarins often exhibit towards unfamiliar, unrelated conspecifics (Prescott, pers. obs.), it was necessary to form the intra-specific averse and non-averse pairs from family troops. These invariably consisted of an adult male-female pair and their juvenile offspring (only juveniles were available at the time of experimentation), hence individuals ranged in age from 8 - 13 months (juveniles) to 5 - 14 years 1 month (adults) at the time of testing. Normally maintained in family troops, adults and offspring were separated only when necessary according to the experimental protocol.

6.2.2 Design

The experimental design required two pairs of individuals, one pair of each species, to each hold contrasting information about the palatability of a preferred target food. First, family troops were split into their respective adult and juvenile pairs and food preference trials conducted for each separately to establish a suitable preferred and less-preferred food. Immediately following these, the adult and juvenile pairs were re-united until it was time to start the conditioning trials (generally three weeks later) when they were separated once again. Conditioning trials were conducted to induce an aversion to the preferred food in a pair of one age class (the averse pair) by altering its taste with table salt (NaCl). Its conspecific pair (of the other age class), meanwhile, received training trials to ensure that their preference for the preferred food was maintained (the non-averse pair). Conditioning and training trials continued for 4 - 6 days (until conditioning and training criteria where reached) which meant that the pairs were kept separated and not re-united until the interactive test trial. Finally, test trials were conducted during which both pairs were given a choice between the preferred food (unadulterated) and the less-preferred food under three conditions: pre-interactive (the averse and non-averse pair alone); interactive (the averse and non-averse pair together); and post-interactive (the averse and non-averse pair again alone, the day after the interactive condition). The behaviour of both averse and non-averse individuals was compared between conditions to see if any change occurred in the preference of either as a result of interaction with their conspecifics.

The experiment was conducted between May and September, 1997. The species were tested in male-female pairs to minimise the stress of separation and more closely resemble the social foraging environment of the wild. The experimental design was counterbalanced for age (within and between species), in that, for each species, one pair of aversely-conditioned juveniles interacted with one pair of non-averse adults, and one pair of aversely-conditioned adults interacted with one pair of non-averse juveniles. The following procedure is described for the former, and is identical for the latter but for age class reversal. Testing juveniles allowed me to examine for an age effect between the two different age classes. It is likely that naïve inexperienced young obtain a greater benefit from learning from others about the palatability of food than do older animals (see Section 3.3). Therefore, one might expect social influences on feeding to be more pronounced in juvenile than in adult monkeys and for younger monkeys to exploit the experience of older monkeys more than vice-versa.

6.2.3 Procedure

All food preference trials, training/conditioning trials, and test trials were conducted in the indoor portions of the tamarins' enclosures before their daily feed to ensure they were motivated to taste the food items.

Food Preference Trials

The experiment required the identification of a food highly preferred by the majority of study animals and one less-preferred. Based upon a knowledge of the tamarins' food preferences in day to day husbandry situations, I selected pieces of glacé cherry as the preferred food item and pieces of peeled apple as the less-preferred food item. Both foods were reasonably familiar to the tamarins (apples were regularly part of the normal rations of the tamarins and glacé cherries were presented less frequently as treats or lures). This initial assessment of food types was validated with food preference tests during which all bar one individual selected and ate the cherry pieces before the apple pieces. Three weeks prior to experimentation, and for the duration of the experiment, these two foods were cut from the monkeys' daily rations.

(1a) *Training for Adults*

The adult male-female pair of each family troop were isolated from their troop-mates in the indoor portion of their enclosure and presented with the two different types of food, ten pieces of each, placed in separate bowls (16 cm in diameter) situated against opposite cage walls. The position of the two different food types (left bowl or right bowl) was alternated in each consecutive presentation and counterbalanced across troops throughout the experiment. Pieces were of approximately equal size (quartered glacé cherries and 1 cm^3 pieces of apple). Recording onto a checksheet began the moment the food was placed in the enclosure and an electronic metronome, audible only to the experimenter via headphones, started. Recording sessions lasted 10 minutes in which one-zero sampling (Martin & Bateson, 1986) was used to record, every 10 seconds, if a food item was eaten, of which type, and by whom during the preceding 10 second sample-interval. One-zero sampling was used because only a simple measure of food preference was required. Trials were repeated, on successive days, until the following criterion was satisfied for three consecutive days: the cherry pieces must have been eaten for more than 75% of the intervals in which each individual was observed to eat. The criterion did not count when one of the two foods was finished before the other (because the animals can only be said to make a choice when both foods are available). This criterion was reached for all individuals in a maximum of three presentations.

(1b) *Aversive Conditioning for Juveniles*

The juvenile male-female pair of each family troop were isolated from their troop-mates in the indoor portion of their enclosure and presented, in 10 minute aversive-conditioning trials, with the same two foods presented to the adult pair. However, the preferred food (cherry) had been made distasteful by soaking the pieces in saturated salt solution for 1 minute and leaving to dry for 15 minutes. Data were collected on who ate what as in (1a). These aversive conditioning trials were repeated, on successive days, until the following criterion was satisfied for three consecutive days: the altered food must have been eaten for less than 25% of the intervals in which each individual was observed to eat. The criterion did not count when the non-altered food was finished before the altered one.

Furthermore, it was important that, as a sign of the learned aversion, at the beginning of the trial, the two juveniles went first to the non-altered food. This criterion was reached for all individuals in a maximum of six presentations.

Test Trials

(2) *Pre-interactive Condition*

Following satisfaction of the criteria described above, the adult and juvenile male-female pairs received a single test trial, in their respective indoor areas. For the adults, this test procedure was identical to their training procedure: ten pieces of the preferred food were placed in one bowl and ten pieces of the less-preferred food in the other. For the juveniles, the test procedure was identical to their training procedure except that the preferred food (which they had learned to avoid during training) were presented *unadulterated*. This was done to test that the juveniles had indeed acquired an aversion, and were not simply responding to possible olfactory cues with regards adulteration of the food. Visual cues were assumed unimportant since the salt was completely absorbed into the fruit pulp and it was not possible for me to discriminate between the adulterated and unadulterated food on the basis of vision. The pre-interactive test trial lasted until all the food items had been eaten or for a maximum of 10 minutes.

(3) *Interactive Condition*

Immediately following the pre-interactive condition, the adult and juvenile male-female pairs were re-united to form a family troop of four individuals. The following day, the family troop received a single test trial in one of their indoor areas (this was counterbalanced between species) during which they were presented with the two food types unadulterated as in (2) except that, because there were now four individuals, twenty items of each type were presented in the two separate bowls. The interactive test trial lasted until all food items had been eaten or for a maximum of 10 minutes.

(4) *Post-interactive Condition*

Immediately following the interactive condition, the pairs were separated again, into adult and juvenile male-female pairs, and the following day, each received a single test trial as in (2). Again, the post-interactive test trial lasted until all food items had been eaten or for a maximum of 10 minutes.

6.2.4 Recording Methods

Test Trials

Data were collected for both averse and non-averse individuals in all three experimental conditions. For all test trials, THE OBSERVER 3.0 event recording computer-program (Noldus, 1993), run on a hand-held computer, was used to record all instances in which an individual ate a food item, of which type and, automatically via the event recorder, the time at which this behaviour was performed (all-occurrences sampling: Altmann, 1974). I also recorded all instances of food transfer and any competitive interactions (food stealing, agonistic behaviour and displacements: see Table 4.5), together with the identity of the individuals involved, *ad libitum*.

For the interactive test trial, because there were now four individuals to observe, a video-camera was used to record the behaviour of the monkeys at the bowl which contained the food type about which the pairs had conflicting information concerning its palatability. At the same time, using the hand-held computer, I recorded the behaviour of the monkeys at the other bowl. Data from the video-tapes were transcribed onto record sheets, directly comparable to those formed from data transcribed from the hand-held computer. (The real-time clock on the video-camera was used to note the time at which each of the behaviours recorded onto the video-tape occurred). Scoring of the video-tapes, in conjunction with the computer data, allowed me to see which food type each individual of each age class went to first in the interactive condition and the pattern thereafter (e.g., if the juveniles follow the adults to the bowl which contains the food they (the juveniles) had learned to avoid).

6.2.5 Data Analysis

For all individuals (averse and non-averse) in the pre-interactive, interactive and post-interactive conditions, I calculated their consumption of the preferred and less-preferred food (the number of pieces they ate of either) and the latencies (in seconds) for them to eat their first piece of each food type. Consumption for each food type was standardised by calculating only the number of pieces of each food taken while both were still available (i.e., I discarded the 'eats' from the remaining food type, after the other food type was finished). Competitive interactions were too infrequent to be included in any meaningful statistical analysis and no instances of food transfer were observed.

The consumption of preferred and less-preferred food, and the latency to eat the first piece of either were analysed separately, across conditions, using the Repeated Measures ANOVA. Significance was set at alpha < 0.05. A-priori pairwise multiple comparisons were made using the Bonferroni method [1].

Comparison of the data for the averse individuals in the pre-interactive condition with that for the interactive and post-interactive conditions enables one to see whether the presence of a non-averse conspecific pair alters consumption of, or latency to consume, either food [2]. Analysis for both the preferred and less-preferred food was conducted to see what the consequences of a change in the preference for one might be on the other (e.g., if non-averse juveniles eat the less-preferred food as a result of monopolisation of the preferred food by the averse adults in the interactive condition).

6.3 Results

Repeated Measures ANOVAs, utilising the whole data set (i.e., collapsing across all three conditions) revealed a significant effect for species in the latency to consume the preferred food by averse individuals, and the latency to consume and consumption of the less-preferred food by non-averse individuals (Table 6.1). Consequently, when examining for differences between conditions for these groups, species was entered into the Repeated Measures ANOVA as a factor.

---

[1] There is some dubiety as to whether, following significant main effects of within subject factors, the Tukey test affords sufficient protection against inflation of the *per family* type I error rate. In the Bonferroni method, ordinary t-tests are used for pairwise comparisons, but the *per family* error rate (0.05) is divided by the number of planned comparisons. To achieve significance, therefore, each test must show significance beyond the 0.05 level (in this case, since there are three possible pairwise comparisons, beyond the 0.05 / 3 = 0.02 level, approximately).

[2] Note that the latency to consume the food is likely to be the more salient measure of the overcoming of the food aversion than is food consumption, because it is a precise measure of the reluctance to eat the averse food initially. Consumption is a less salient measure because averse individuals are highly likely to start to consume the unadulterated preferred food once they have tasted their first piece of it and realised that it is palatable. Comparisons of consumption between conditions are thus less likely to give significant differences than are comparisons of latency, if indeed the monkeys are learning from each other.

Table 6.1: Repeated Measures ANOVA F-values and mean scores for species differences in the latency (seconds) to consume, and consumption (number of pieces) of, the preferred and less-preferred food by averse and non-averse individuals.

Individuals	**Measure**	**Food Type**	**Species (*S. fuscicollis* / *S. labiatus*)**
Averse	Latency	Preferred food	$F_{1,6} = 9.43$, $\mathbf{p < 0.05}$ (211 , 69)
		Less-preferred food	$F_{1,6} = 0.06$, $p > 0.05$ (137 , 131)
	Consumption	Preferred food	$F_{1,6} = 3.95$, $p > 0.05$ (2.00 , 2.42)
		Less-preferred food	$F_{1,6} = 5.55$, $p > 0.05$ (3.08 , 2.08)
Non-averse	Latency	Preferred food	$F_{1,6} = 0.35$, $p > 0.05$ (17 , 21)
		Less-preferred food	$F_{1,6} = 7.08$, $\mathbf{p < 0.05}$ (157 , 372)
	Consumption	Preferred food	$F_{1,6} = 0.65$, $p > 0.05$ (3.67 , 4.08)
		Less-preferred food	$F_{1,6} = 10.72$, $\mathbf{p < 0.05}$ (1.75 , 0.50)

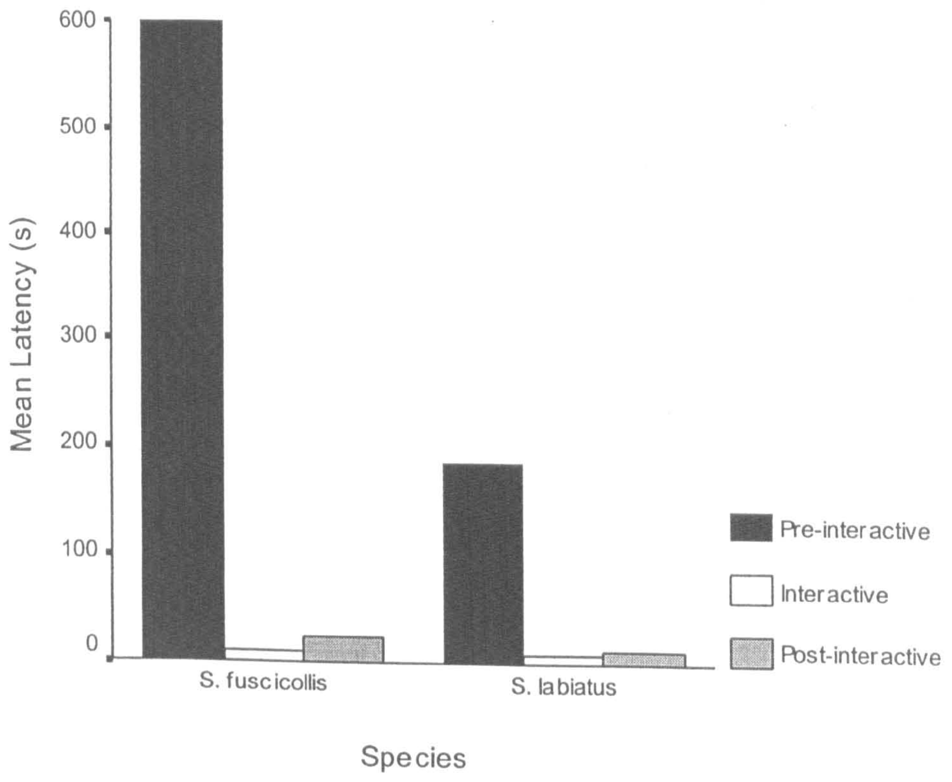
Bold indicates a significant result.

Averse individuals

There was a significant effect for condition ($F_{2,12} = 19.49$, $p < 0.05$), a significant effect for species ($F_{1,6} = 9.43$, $p < 0.05$), and a significant interaction between condition and species ($F_{2,12} = 8.24$, $p < 0.05$; Figure 6.1) in the latency to consume the **preferred food** by averse individuals.

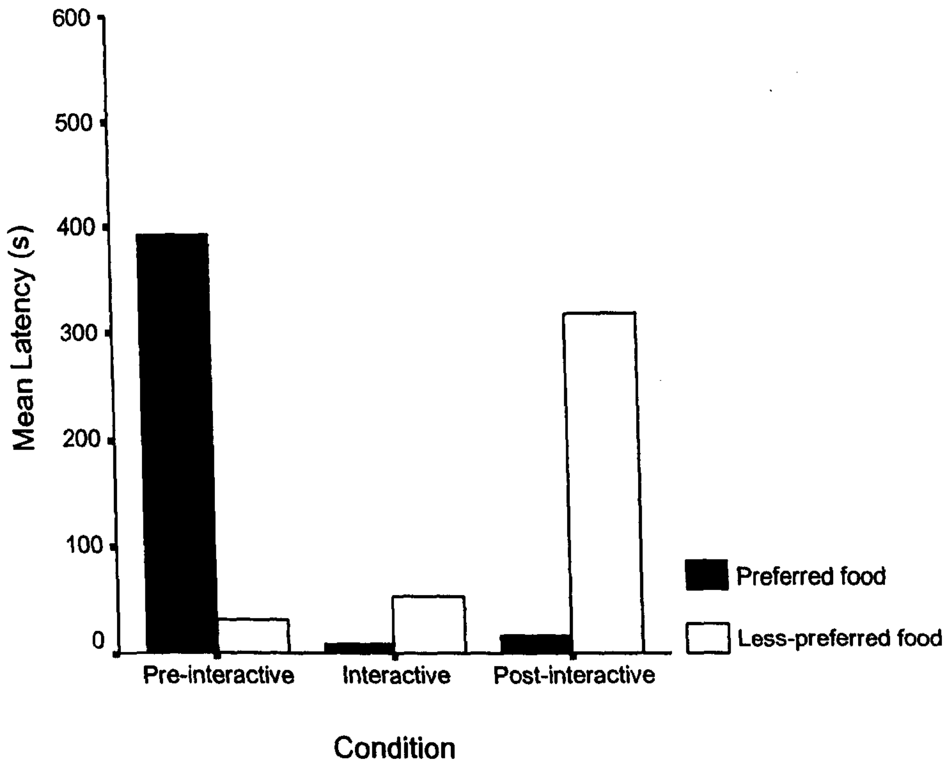
The latency with which averse *S. fuscicollis* ate the preferred food was found to differ between conditions ($F_{2,6} = 3106.93$, $p < 0.05$). Averse *S. fuscicollis* were slower to eat the preferred food in the pre-interaction than they were in the interactive condition ($p < 0.05$) and post-interaction condition ($p < 0.05$). The latency with which averse *S. labiatus* ate the preferred food, however, was found not to differ between conditions ($F_{2,6} = 1.54$, $p > 0.05$).

Figure 6.1: Mean latencies (seconds) to consume the preferred food by averse *S. fuscicollis* and averse *S. labiatus* in the pre-interactive, interactive and post-interactive conditions.



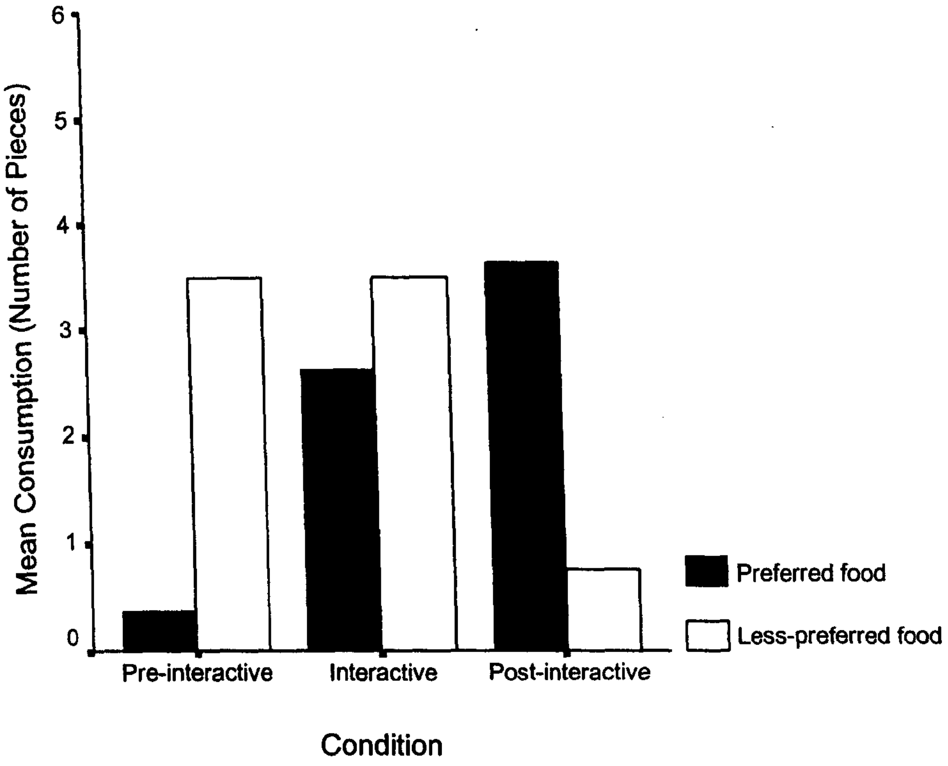
The latency with which averse individuals ate the **less-preferred food** was also found to differ between conditions ($F_{2,14} = 6.81$, $p < 0.05$; Figure 6.2). However, Bonferroni pair-wise comparisons revealed only a non-significant trend for faster consumption of the less-preferred food pre-interaction than post-interaction ($p > 0.05$).

Figure 6.2: Mean latencies (seconds) to consume the preferred and less-preferred food by averse individuals in the pre-interactive, interactive and post-interactive conditions.



Consumption of the **preferred food** by averse individuals was found to differ between conditions ($F_{2,14} = 23.87$, $p < 0.05$; Figure 6.3). Averse individuals ate more of the preferred food in the presence of non-averse conspecifics than they did in their absence pre-interaction ($p < 0.05$). This preference was maintained in the post-interactive condition ($p < 0.05$). Consumption of the **less-preferred food** by averse individuals was found not to differ between conditions ($F_{2,12} = 4.39$, $p > 0.05$).

Figure 6.3: Mean consumption (number of pieces) of the preferred and less-preferred food by averse individuals in the pre-interactive, interactive and post-interactive conditions.



<u>*Non-averse individuals*</u>

The latency with which non-averse individuals ate the **preferred** food did not differ between conditions ($F_{2,12} = 0.26$; $p > 0.05$; Figure 6.4). There was a significant effect for condition ($F_{2,14} = 6.14$; $p < 0.05$), a significant effect for species ($F_{1,7} = 21.98$; $p < 0.05$), but no significant interaction between condition and species ($F_{2,14} = 0.04$; $p > 0.05$; Figure 6.5) in the latency with which non-averse individuals ate the **less-preferred food**. However, when broken down by species, neither species exhibited a significant effect for condition ($F_{2,7} = 0.57$; $p > 0.05$, for *S. fuscicollis*; $F_{2,7} = 0.05$; $p > 0.05$, for *S. labiatus*).

Figure 6.4: Mean latencies (seconds) to consume the preferred and less-preferred food by non-averse individuals in the pre-interactive, interactive and post-interactive conditions.

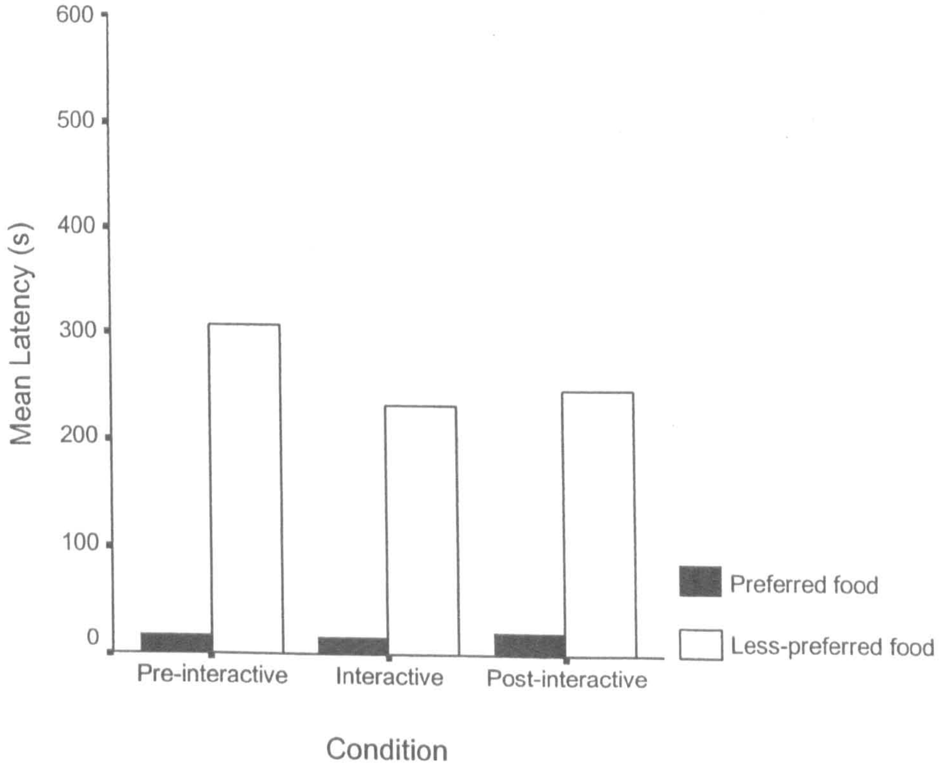
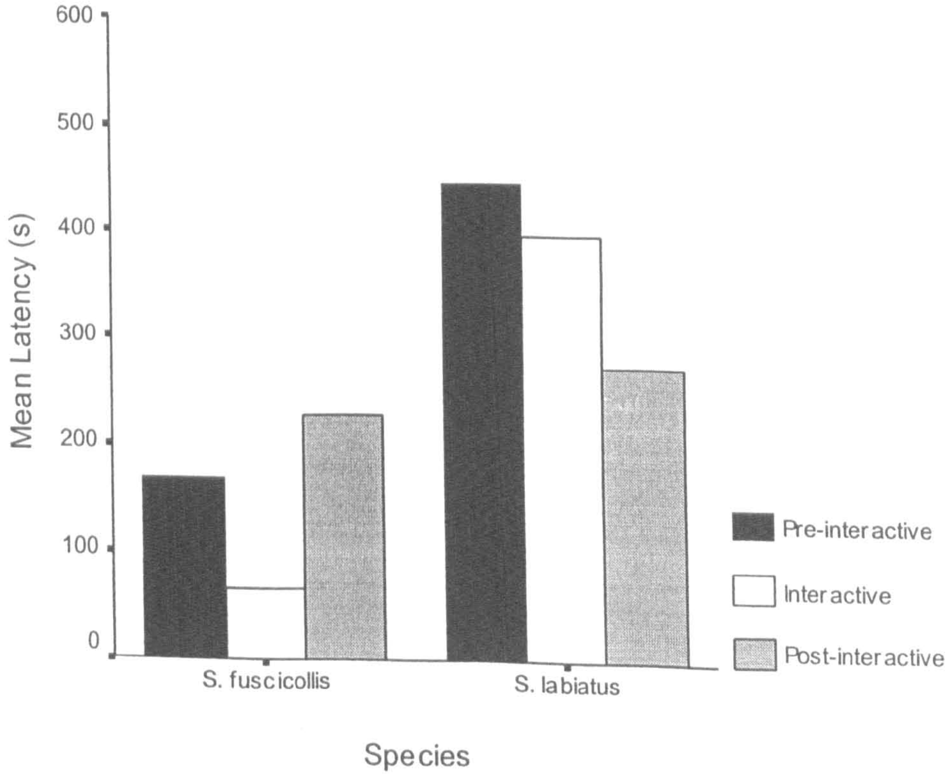
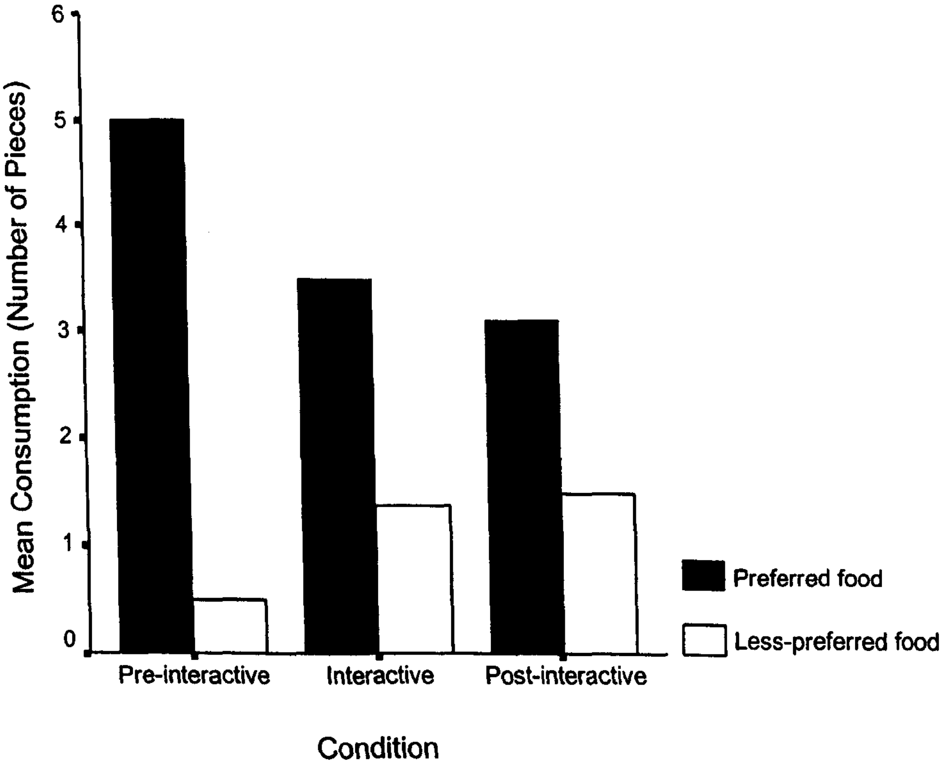


Figure 6.5: Mean latencies (seconds) to consume the less-preferred food by non-averse *S. fuscicollis* and non-averse *S. labiatus* in the pre-interactive, interactive and post-interactive conditions.



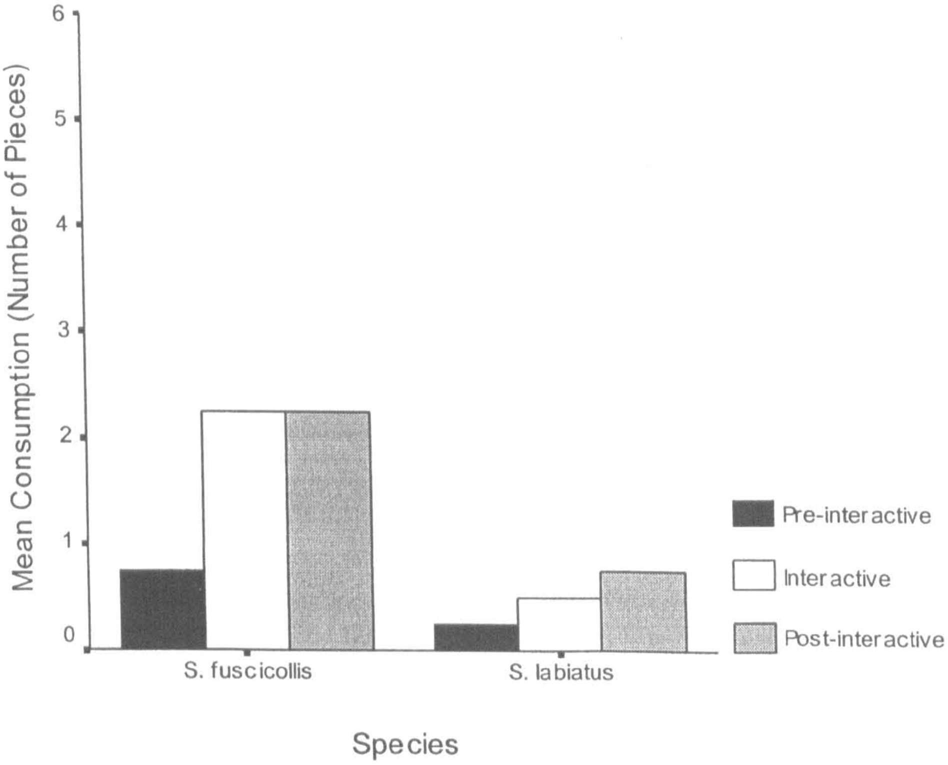
Consumption of the **preferred food** by non-averse individuals was found to differ between conditions ($F_{2,14} = 7.74$, $p < 0.05$; Figure 6.6). Non-averse individuals ate more of the preferred food pre-interaction than they did post-interaction ($p < 0.05$). A non-significant trend for greater consumption of the preferred food in the pre-interactive than interactive condition was also observed ($p > 0.05$).

Figure 6.6: Mean consumption (number of pieces) of the preferred and less-preferred food by non-averse individuals in the pre-interactive, interactive and post-interactive conditions.



There was a significant effect for condition ($F_{2,12} = 8.24$, $p < 0.05$), a significant effect for species ($F_{1,6} = 10.72$, $p < 0.05$), but no interaction between condition and species ($F_{2,12} = 1.11$, $p > 0.05$; Figure 6.7), for consumption of the **less-preferred food** by non-averse individuals. Consumption of the less-preferred food was found to differ between conditions for *S. fuscicollis* ($F_{2,6} = 27.00$; $p < 0.05$). Bonferroni pairwise comparisons revealed greater consumption of the less-preferred food in the interactive than pre-interactive condition ($p > 0.05$). Consumption of the less-preferred food did not differ between conditions for *S. labiatus* ($F_{2,6} = 0.27$; $p > 0.05$).

Figure 6.7: Mean consumption (number of pieces) of the less-preferred food by non-averse *S. fuscicollis* and non-averse *S. labiatus* in the pre-interactive, interactive and post-interactive conditions.



So it appears that, in general, in the interactive condition, averse individuals are facilitated by their non-averse conspecifics to eat the unadulterated preferred food having avoided it in the pre-interactive condition. This facilitatory effect was apparent for both species for consumption, but only for *S. fuscicollis* for latency.

Repeated Measures ANOVAs, pooling species, revealed a significant difference between age classes (i.e., averse juveniles interacting with non-averse adults, and averse adults interacting with non-averse juveniles) in the pattern of their latency to consume the **preferred food** ($F_{1,6} = 9.43$, $p < 0.05$; Table 6.2) across conditions. There was no significant difference in the pattern of their latency to consume the **less-preferred food** ($F_{1,6} = 0.01$, $p > 0.05$).

Table 6.2: Mean latencies (seconds) to consume preferred and less-preferred food for averse juveniles (interacting with non-averse adults), and averse adults (interacting with non-averse juveniles).

Condition	**Age Class**	**n**	**Preferred Food**		**Less-preferred Food**	
			Mean	SD	Mean	SD
Pre-interactive						
	Juveniles	4	186.25	280.84	38.25	56.52
	Adults	4	600.00	0.00	26.00	19.53
Interactive						
	Juveniles	4	8.75	3.86	39.00	13.49
	Adults	4	10.25	2.75	66.50	18.48
Post-interactive						
	Juveniles	4	24.00	21.60	316.00	327.94
	Adults	4	12.50	8.66	319.25	324.66

Nor were there any significant differences between age classes in the pattern of consumption of the **preferred food** ($F_{1,6} = 3.95$, $p > 0.05$) or **less-preferred food** ($F_{1,6} = 5.54$, $p > 0.05$; Table 6.3) across conditions by averse individuals.

Table 6.3: Mean consumption (number of items) of preferred and less-preferred food for averse juveniles (interacting with non-averse adults), and averse adults (interacting with non-averse juveniles).

Condition	**Age Class**	**n**	**Preferred Food**		**Less-preferred Food**	
			Mean	SD	Mean	SD
Pre-interactive						
	Juveniles	4	0.75	0.50	5.00	0.00
	Adults	4	0.00	0.00	2.00	2.00
Interactive						
	Juveniles	4	2.25	1.26	3.25	1.71
	Adults	4	3.00	0.82	3.75	1.51
Post-interactive						
	Juveniles	4	4.25	0.50	1.00	1.15
	Adults	4	3.00	0.82	0.50	0.58

6.4 Discussion

Comparison of the latency to consume, and consumption of, both food types in the pre-interactive condition with that in the interactive and post-interactive conditions enabled me to see whether a spontaneous preference for the preferred food shown in a pair of one species could modify an induced aversion to that same food in a pair of conspecifics. The fact that neither food type was adulterated in the three test conditions enables me to attribute any change in food preference for the averse individuals to the social interaction itself, rather than to any olfactory or visual cues.

Non-averse individuals showed no difference in their latencies to the preferred food and less-preferred food across conditions, but for the aversely conditioned individuals, the sudden change in social context corresponded to a change in their preference for the preferred food. That is, they increased their consumption of the preferred food (but not the less-preferred food) during and following interaction with their non-averse conspecifics. This provides evidence that the aversely conditioned individuals learnt from interaction with their non-averse conspecifics that the food they had been conditioned to think was unpalatable was now palatable again. Queryas and Vitale (pers. comm.) found the same result with conspecific pairs of marmosets (*C. jacchus*). These findings are also in line with what is found in conspecific groups of *R. norvegicus* and *C. crocuta*: social interaction with non-averse individuals promotes the extinction of an aversion to a target food (Galef, 1986; Yoerg, 1991). Further evidence of this effect is provided for averse *S. fuscicollis* by their latency scores. Averse *S. fuscicollis* were quicker to the preferred food (and slower to the less-preferred food) during and following interaction with their non-averse conspecifics. Averse *S. labiatus*, on the other hand, showed no difference in their latency to consume the preferred food (or less-preferred food) across conditions. The lack of a significant difference in the latency to consume the preferred food for averse *S. labiatus* was due to the fact that three out of the four averse *S. labiatus* tried the (unadulterated) preferred food in the pre-interactive condition before interaction with their non-averse conspecifics. These three individuals were two 12 month old juveniles (a male and female) and an old female (14 years 1 month). Curiosity in juvenile primates has been noted by many authors, whereas adults, in comparison, are generally considered conservative due to the accumulation of experience (Menzel, 1969; Kummer 1971; Goodall, 1973). (As we shall see in Experiment 3, where all the study animals were adults (> 2 years old), most did not try the unadulterated preferred food (that they had been trained to think distasteful) before interaction with non-averse congeners). The fact that these juvenile *S. labiatus* tried the preferred food in the pre-interactive condition meant that there was a significant difference between age classes in the pattern of their latency to consume the preferred food across conditions. No other age effects were found. In a very similar experiment, Queyras and Vitale (pers. comm.) found no significant differences between individual *C. jacchus* of different age classes.

There was a non-significant trend for greater consumption of the preferred food by non-averse individuals in the pre-interactive condition than in the presence of their averse conspecifics. It is likely that this was a result of competition for the preferred food in the interactive condition from their averse conspecifics (once they had learnt that the preferred food was again palatable). Non-averse *S. labiatus* showed no difference in their consumption of the less-preferred food across conditions. They, in fact, ate very little of the less-preferred food in any condition. Non-averse *S. fuscicollis*, however, ate more of the less-preferred food in the interactive condition than in the pre-interactive condition. This too is likely to be due to competition from their averse conspecifics for the preferred food, forcing them to eat more of the less-preferred food instead.

I expected to see some instances of food sharing, given that the interactants were related and that the preferred food was rare and highly prized. Food sharing would appear to be an excellent way for juveniles to learn about the palatability of food items from other troop members, thereby avoiding experimentation with potentially harmful food stuffs. However, food sharing was not observed (nor was it observed in Experiment 3). Nor was there any evidence of teaching, in that knowledgeable non-averse individuals did not alter their behaviour in accordance with the knowledge state of the averse individuals, even though they were related. This is in line with the literature for non-human primates, where pedagogical abilities are apparently not required for the normal subsistence activities of monkeys (Visalberghi & Fragaszy, 1996). Instead, non-averse individuals appeared to do what they would do anyway in the absence of interaction, and in doing so, provided clues or motivational influences that aided the averse individuals to learn for themselves the change in the palatability of the preferred food.

So the opportunity to learn from conspecific troop-mates about the palatability of food is likely to be an advantage of sociality to both species in that they can benefit from the knowledge of their conspecifics. If species are able to learn this information from their congeners also, then mixed-species troops would be an advantage over single-species troops in that both species would have access to an increased knowledge base (that of their own species and of the associating species). To examine for social learning about the palatability of food between congeners, I repeated the experiment but with inter-specific pairs of interactants (Experiment 3). This has the additional interest that, if species learn better from their congeners than from their own species, then the formation of mixed-species troops would be additionally beneficial over similarly-sized monospecific ones. Let us now turn to Experiment 3 in order to explore these propositions.

6.5 Experiment 3: Inter-Specific Social Enhancement of the Extinction of a Food Aversion

Experiment 3 was very similar to Experiment 2, except that, rather than investigating inter-specific information transfer between conspecific pairs, information transfer was investigated between pairs of congeners. By comparing the results of this experiment with those of Experiment 2, a comparison can be made between intra-specific and inter-specific interactants to see whether one or both species are more likely to acquire information pertaining to the palatability of different food types from their congeners than from their own species. This would indicate an additional advantage to forming mixed-species troops, over and above that accrued simply because of the increased opportunity for information transfer as a result of the increase in troop size in a mixed-species troop.

The aim of the experiment was to investigate whether the presence of a congener could influence food choice. Specifically, it investigated whether a spontaneous preference for a particular food shown in a pair of one species could influence an induced aversion to that same food in a pair of congeners.

6.5.1 Study Animals

The study animals were adult male-female pairs taken from six troops of *S. fuscicollis* (SF3, SF5 ,SF7, SF9, SF10, SF11: Table 4.3) and six troops of *S. labiatus* (SL2, SL5, SL7, SL9, SL10, SL11: Table 4.4) housed in separate indoor/outdoor enclosures in the 'Old Marmoset-House'. Further details of housing and husbandry are given in Chapter 4 (Section 4.6). The monkeys' ages were similar across species and ranged from 1 year 7 months to 9 years 6 months at the time of testing. The troops were normally maintained as mixed-species troops (SF3 & SL11, SF5 & SL5, SF7 & SL7, SF9 & SL9, SF10 & SL10, SF11 & SL2) and were separated into adjacent enclosures only when necessary according to the experimental protocol.

6.5.2 Design

The experimental design was as in Experiment 2 (see Section 6.2.2), except that each pair of each species interacted with a congeneric pair as opposed to a conspecific pair. The experimental design was counterbalanced between species, in that, three male-female pairs of *S. labiatus* each received the aversive conditioning and then interacted with three non-averse pairs of *S. fuscicollis*; and three male-female of *S. fuscicollis* received the aversive conditioning and then interacted with three non-averse pairs of *S. labiatus*. The experiment was conducted almost simultaneously with Experiment 2, between April and September, 1997.

6.5.3 Procedure

The experimental procedure was exactly that of Experiment 2 (see Section 6.2.3), except that, averse adult pairs had the opportunity to interact with non-averse congeneric adult pairs as opposed to non-averse conspecific adult or juvenile pairs. Again, all training and test trials were conducted in the indoor portions of the tamarins' enclosures, before the tamarins' daily feed to ensure they were motivated to taste the food items.

6.5.4 Recording Methods

Recording methods were exactly as those in Experiment 2 (see Section 6.2.4).

6.5.5 Data Analysis

Data analysis was exactly as that in Experiment 2 (see Section 6.2.5), using Repeated Measures ANOVAs with significance set at alpha < 0.05. However, note that, in addition to the inter-specific results for this experiment, Section 6.6 also presents the results of statistical comparisons (using the Repeated Measures ANOVA) between the inter-specific data from this experiment (Experiment 3) and the intra-specific data from Experiment 2. Again, to control for the possibility of making type I errors over the set of three pairwise comparisons, according to the Bonferroni method, I considered a significance level of 0.02 (= 0.05 / 3).

6.6 Results

Repeated Measures ANOVAs, utilising the whole data set (i.e., collapsing across all three conditions) revealed no main effect for species in either the latency to consume the preferred food or less-preferred food, or in the consumption of the preferred food or less-preferred food, for averse and non-averse individuals (Table 6.4). Therefore, the results presented below are for the data set pooled for species.

Table 6.4: Repeated Measures ANOVA F-values and mean scores for species differences in the latency (seconds) to consume, and consumption (number of pieces) of, the preferred and less-preferred food by averse and non-averse individuals.

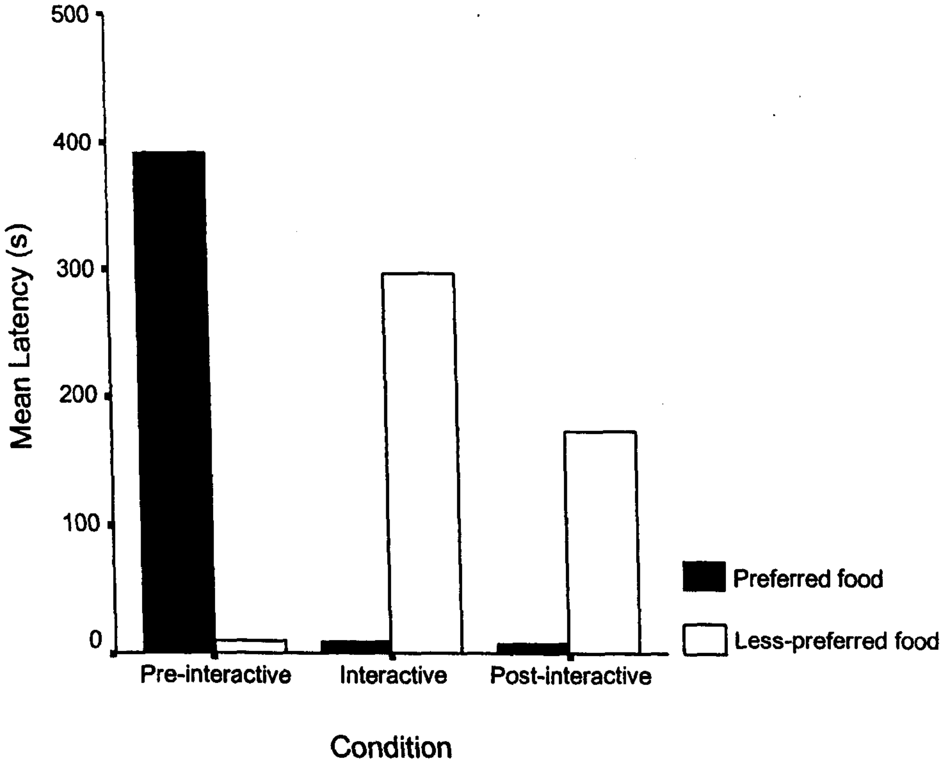
Individuals	**Measure**	**Food Type**	**Species (*S. fuscicollis/S. labiatus*)**
Averse	Latency	Preferred food	$F_{1,10} = 1.42, p > 0.05$ (115 , 159)
		Less-preferred food	$F_{1,10} = 1.01, p > 0.05$ (156 , 164)
	Consumption	Preferred food	$F_{1,10} = 1.20, p > 0.05$ (3.83 , 3.89)
		Less-preferred food	$F_{1,10} = 1.10, p > 0.05$ (3.61 , 3.33)
Non-averse	Latency	Preferred food	$F_{1,10} = 1.04, p > 0.05$ (11 , 14)
		Less-preferred food	$F_{1,10} = 2.00, p > 0.05$ (259 , 370)
	Consumption	Preferred food	$F_{1,10} = 0.74, p > 0.05$ (4.89 , 5.51)
		Less-preferred food	$F_{1,10} = 0.01, p > 0.05$ (1.78 , 1.83)

Averse individuals

The latency with which averse individuals ate the **preferred food** was found to differ between conditions ($F_{2,22}$= 47.79, $p < 0.05$; Figure 6.8). Averse individuals were slower to eat the preferred food in the pre-interaction condition than they were in the interactive condition ($p < 0.05$) and post-interactive condition ($p < 0.05$).

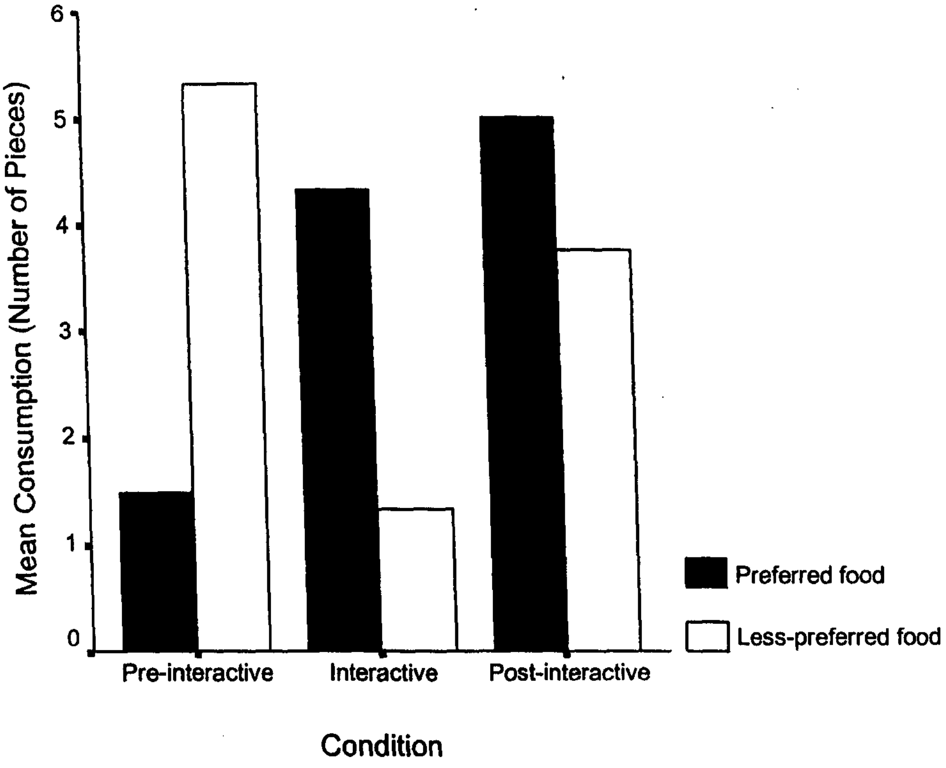
The latency with which averse individuals ate the **less-preferred food** was also found to differ between conditions ($F_{2,22} = 10.86$, $p < 0.05$). Averse individuals were quicker to eat the less-preferred food in the pre-interactive condition than in the interactive condition ($p < 0.05$). Comparing latencies for the pre-interactive and post-interactive conditions, there was a non-significant trend for reduced latency in the pre-interactive condition ($p > 0.05$).

Figure 6.8: Mean latencies (seconds) to consume the preferred and less-preferred food by averse individuals in the pre-interactive, interactive and post-interactive conditions.



Consumption of the **preferred food** by averse individuals was found to differ between conditions ($F_{2,22} = 27.54$, $p < 0.05$; Figure 6.9). Averse individuals ate more of the preferred food in the presence of non-averse congeners (interactive condition) than they did pre-interaction ($p < 0.05$). This preference was maintained in the post-interactive condition ($p < 0.05$). Consumption of the **less-preferred food** by averse individuals was also found to differ between conditions ($F_{2,22} = 22.34$, $p < 0.05$). Averse individuals ate more of the less-preferred food prior to interacting with non-averse congeners than they did during the interactive condition ($p < 0.05$) and post-interaction ($p < 0.05$).

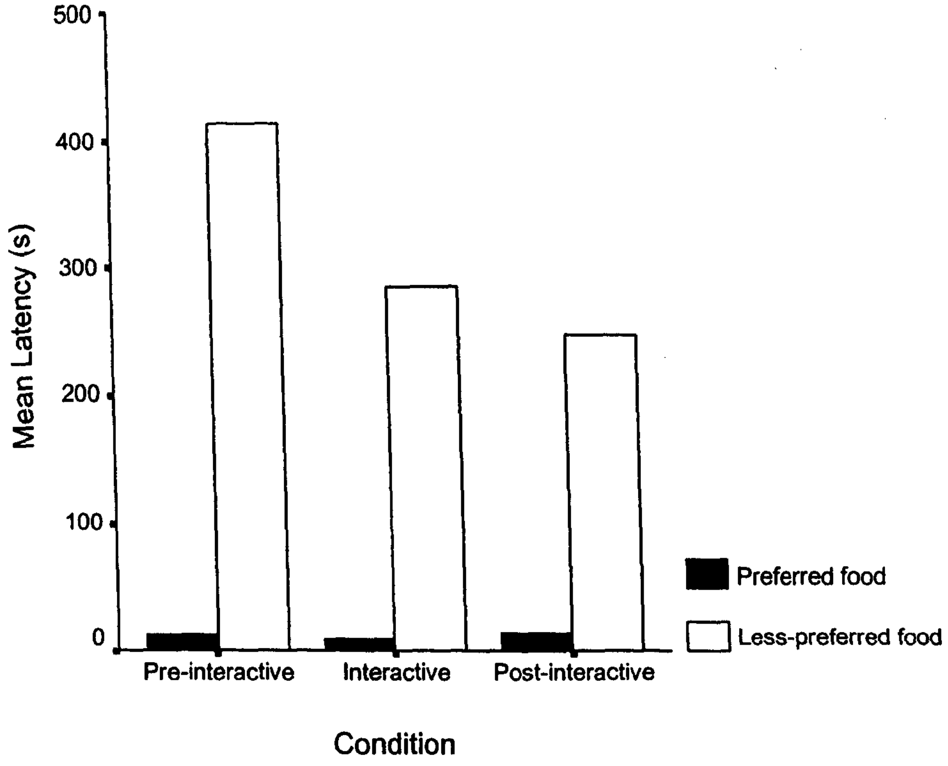
Figure 6.9: Mean consumption (number of items) of the preferred and less-preferred food by averse individuals in the pre-interactive, interactive and post-interactive conditions.



Non-averse individuals

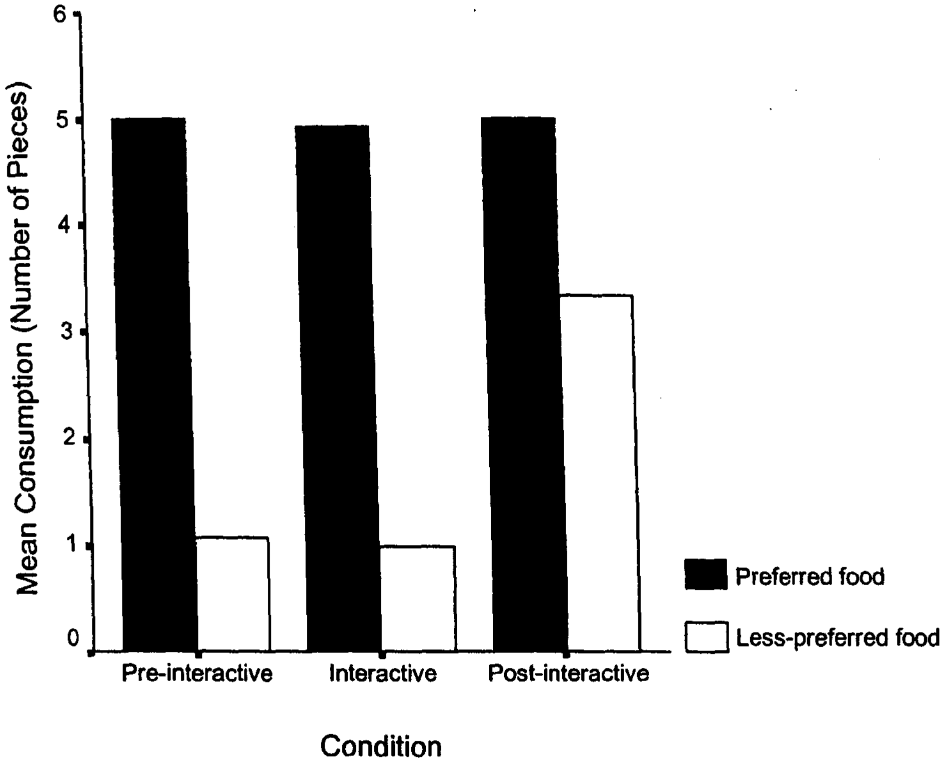
The latency with which non-averse individuals ate the **preferred food** did not differ between conditions ($F_{2,22} = 1.03$; $p > 0.05$; Figure 6.10). Nor did the latency with which non-averse individuals ate the **less-preferred food** ($F_{2,22} = 1.91$; $p > 0.05$).

Figure 6.10: Mean latencies (seconds) to consume the preferred and less-preferred food by non-averse individuals in the pre-interactive, interactive and post-interactive conditions.



Consumption of the **preferred food** by non-averse individuals did not differ between conditions ($F_{2,22} = 0.04$; $p > 0.05$; Figure 6.11). Nor did consumption of the **less-preferred food** ($F_{2,22} = 2.10$; $p > 0.05$).

Figure 6.11: Mean consumption (number of items) of the preferred and less-preferred food by non-averse individuals in the pre-interactive, interactive and post-interactive conditions.



It appears then, that in the interactive condition, averse individuals are socially facilitated by their non-averse congeners to eat the unadulterated preferred food that they avoided in the pre-interactive condition, whereas non-averse individuals are unaffected by the averse congeners. We can now go on to examine whether this facilitation is symmetrical between species; that is, do averse *S. fuscicollis* learn more quickly from non-averse *S. labiatus* than do averse *S. labiatus* from non-averse *S. fuscicollis*, or vice versa?

There were no significant differences between species (i.e., averse *S. fuscicollis* interacting with non-averse *S. labiatus*, and averse *S. labiatus* interacting with non-averse *S. fuscicollis*) in the pattern of their latency to consume the **preferred food** ($F_{1,10} = 1.42$, $p > 0.05$) or **less-preferred food** ($F_{1,10} = 1.01$, $p > 0.05$; Table 6.5) across conditions.

Table 6.5: Mean latencies (seconds) to consume preferred and less-preferred food for averse *S. fuscicollis* (interacting with non-averse *S. labiatus*), and averse *S. labiatus* (interacting with non-averse *S. fuscicollis*).

Condition	**Species**	**n**	**Preferred Food**		**Less-preferred Food**	
			Mean	SD	Mean	SD
Pre-interactive						
	S. fuscicollis	6	325.83	187.29	9.50	6.09
	S. labiatus	6	460.50	190.42	11.83	4.62
Interactive						
	S. fuscicollis	6	11.00	3.85	349.83	211.36
	S. labiatus	6	9.17	1.33	243.33	276.70
Post-interactive						
	S. fuscicollis	6	9.50	2.66	109.33	54.50
	S. labiatus	6	8.67	3.33	235.50	283.45

Nor were there any significant differences between species in the pattern of consumption of the **preferred food** ($F_{1,10} = 1.20$, $p > 0.05$) or **less-preferred food** ($F_{1,10} = 0.10$, $p > 0.05$; Table 6.6) across conditions by averse individuals. Therefore, any benefit accrued to averse individuals from overcoming the aversion as a result of interaction with non-averse congeners would be symmetrical between species.

Table 6.6: Mean consumption (number of items) of preferred and less-preferred food for averse *S. fuscicollis* (interacting with non-averse *S. labiatus*), and averse *S. labiatus* (interacting with non-averse *S. fuscicollis*).

Condition	**Species**	**n**	**Preferred Food**		**Less-preferred Food**	
			Mean	SD	Mean	SD
Pre-interactive						
	S. fuscicollis	6	2.33	2.251	5.67	2.338
	S. labiatus	6	0.67	0.517	5.00	0.894
Interactive						
	S. fuscicollis	6	4.17	0.753	1.00	0.894
	S. labiatus	6	4.50	1.048	1.67	1.633
Post-interactive						
	S. fuscicollis	6	5.00	0.632	4.17	2.137
	S. labiatus	6	5.00	0.894	3.33	2.875

6.7 Discussion

For the inter-specific interactants in Experiment 3, both the latency and consumption data showed that the opportunity to interact with non-averse congeners led to the extinction of the learned aversion to the preferred food for averse *S. fuscicollis* and averse *S. labiatus*. Furthermore, the extinction was not dependent upon social context in that, when tested one day after interaction, the averse individuals continued to eat the preferred food that they had, previous to interaction, thought distasteful. The preference of the non-averse congeners for the preferred food appeared unaffected by interaction with averse congeners and was, in fact, relatively constant across all three conditions. In the interactive condition, they always reached the preferred food before their aversely conditioned congeners. Thus, averse individuals appeared to learn from the behaviour of their non-averse congeners (that is, the non-averse congeners' constant preference for the preferred food) that what was once palatable and became unpalatable (following conditioning) is now palatable again. The same result was found in Experiment 2 with conspecific pairs; information travelled from non-averse individuals to averse ones.

The re-establishment of the preference for the preferred food in averse individuals was very rapid (a single trial); almost as soon as they saw their non-averse conspecifics or congeners eating the preferred food, they joined them at it and began to eat it also. Furthermore, for all averse individuals, the preferred food that they had been reluctant to eat during the pre-interactive condition was eaten again in the interactive condition. This may have been due to the familiarity of the preferred food. Hikami (1991) has suggested that familiarity with the food that an aversion is created towards can reduce the strength of the aversion, making it easier to extinguish. However, this result is also interesting in the context of tamarins fruit foraging in their natural environment, waiting for known fruit resources to ripen. Note that, as described in Chapter 1, the major fruit resources of tamarins characteristically ripen in a piecemeal fashion (i.e., a little at a time) but over a relatively long period. Since only small amounts are available at any instant in time, there is likely to be considerable pressure to act rapidly and exploit the fruit quickly before other frugivorous competitors do. Garber (1988b) suggests that, for tamarins, first or priority of access to small fruit resources is likely to be a critical factor in foraging success. Piecemeal ripening does of course mean that once they have learnt that a particular tree is ripe, they can then return to that tree as a reliable source of fruit. However, some the fruit species taken by tamarins are of genera that fruit asynchronously within species (e.g., *Ficus*) or between species (e.g., *Inga*) (Peres, 1993b). This means that it is not easy to predict when a particular tree or species is about to come into ripe fruit. Given that the change from unripe to ripe is often very rapid, and given high inter-specific competition for fruit amongst forest frugivores (particularly in the dry season, or in large fruiting trees), observation of conspecifics or congenerics feeding on fruit is likely to be an effective proximate cue signalling ripeness, to which the monkeys ought to respond quickly. The mechanism need not be limited to animals of the same order; avian, sciurid or chirpoteran frugivores may similarly signal ripeness. For example, there is evidence that the calls of *Bycanistes subcylindricus* (black-and-white casqued hornbill) alert *Lophocebus albigena* (gray-cheeked mangabey) to previously unknown fruit resources or, in the case of previously known fruiting trees, to the continued presence of ripe fruit (Olupot *et al.*, 1998). Once within proximity of the fruit, given the amount of cover between foraging individuals, it is possible that they cannot see exactly what species of fruit their troop-mates are consuming, or at what stage of ripeness the fruit is at. However, it is likely that sounds and gross features of behaviour, sufficient to indicate that other troop members are feeding, can be transmitted under these conditions and that these are sufficient to facilitate troop members in the same tree or adjacent trees to try the fruit.

So social interaction (with non-averse conspecifics or congeners) led to the extinction of the induced aversion to the preferred food for averse individuals. However, it could be that, despite their aversion towards it, the averse individuals would have sampled the (unadulterated) preferred food anyway, without the influence of their conspecific or congeneric troop-mates, leading to the re-establishment of their previous preference toward it independent of social influence. In order to test this, I would have had to continue presenting the unadulterated preferred food to the averse individuals in the absence of social interaction with non-averse individuals. Although, some individuals (of both species) did do this in the pre-interactive condition, gaining the knowledge that the preferred food, now unadulterated, was again good to eat, it was found that most did not. (This lends weight to the assumption that visual and olfactory cues indicating adulteration of the food were not present or perceivable to the tamarins). Despite the likelihood that averse individuals would have overcome their aversion over time, the advantage to *social* learning lies in the fact that sociality (interaction) appeared to speed up this process (extinction of the aversion). Thus, although learning that the food is palatable can occur very quickly by trial and error learning, lone individuals might not taste the food at all, whereas in social troops with others eating it, individuals appear facilitated to do so. Such facilitation is likely to increase foraging efficiency relative to each troop member having to continually reassess the quality of food individually. As already described, facilitation of the extinction of food aversion is ecologically relevant with regards to changes in the palatability of food types, particularly ripe fruit, because it acts to increase the speed of their exploitation which may, in turn, reduce intra- and inter-specific exploitation feeding competition. In fact, an ability to respond rapidly to environmental change generally (behavioural plasticity) is likely to be a winning strategy in variable environments where conditions change frequently (e.g., the pronounced dry seasons of the tropics) (Box, 1984). Furthermore, as pointed out by Vitale and Queryas (1997), such a facilitatory tendency would have the long-term function of maintaining variability in the diet of generalist species.

As mentioned earlier, the food preference of non-averse individuals was largely unaffected by interaction with their averse conspecifics or congeners. Furthermore, averse individuals did nothing to prevent the non-averse individuals from eating the food that they (the averse individuals) thought distasteful. This is in line with the absence of examples of teaching (i.e., teaching requiring *intention* and *attribution* on the part of the teacher) about foods in the literature for non-human primates (with the possible exception of the apes: see Tomasello & Call, 1997). It is also in agreement with the scant literature on food preference and avoidance learning in monkeys and apes, where it appears that food preference can be transmitted socially but food avoidance cannot (see Visalberghi, 1994, for a review). Instead, food avoidance appears dependent upon individual experience (Visalberghi & Fragaszy, 1996).

The findings for learning about food preference (rather than food aversion) are in contrast to what is known concerning learning of potential predator avoidance (e.g., Mineka & Cook, 1993, for observational learning of snake fear in *M. mulatta*) where prior individual experience with the predator is not crucial to elicit a fear response. Perhaps the emotive cues given towards a potential predator are more salient or extreme than those given as a consequence of ingestion of distasteful or noxious food (note that, non-human primates generally do not have facial expressions indicating disgust at the taste of food: Visalberghi & Fragaszy, 1996). In response to the unpalatable food, the tamarins simply removed the food item from their mouths and dropped it to the floor, or else let it fall from their mouths. Whatever the case, although asocial learning (individual experience) may be central to food avoidance learning, in this case, the choice to sample the preferred food (for the averse individuals) in the interactive condition was probably based upon an integration of information gathered individually before the aversive conditioning and that gathered socially during the interaction with others. Laland *et al.* (1993), write that

> *"acquisition of a socially learned behaviour can be thought of as a mix of individual experience and social interaction, and its position on this (social/individual learning) dimension is dependent upon the relative weighting given to cues derived from individual experience and social interaction"* (p. 262).

In this case it payed for the aversely-conditioned individuals to restore their preference for the previously preferred food (that they knew to be sweeter than the less-preferred food and thus of higher calorific value) after having seen their conspecifics or congeners eating it. Overall, together with the evidence available from the literature, it appears that, although the origination of particular dietary preferences can best accounted for by socially independent mechanisms (e.g., individual experience of gustatory, olfactory and visual clues, and perception of gastrointestinal events), socially dependent mechanisms (social context) can influence and/or maintain these preferences (e.g., Jouventin *et al.*, 1976; Whitehead, 1986). Whitehead (1986) suggests that in all likelihood, both socially dependent and independent mechanisms are present in monkeys and capable of working in a complementary fashion to ensure foraging competence. In fact, natural selection should act upon a complex of genetic transmission, individual experience, and transmission through social learning, and to optimise over the costs and benefits of each (Laland *et al.*, 1996).

Once again, as in Experiment 1 (Chapter 5), tamarins appear sensitive to the behaviour of their congeners and to make use of the experience of those others to modify their own behavioural responses into a potentially more adaptive direction. But what of the significance of this for mixed-species troops. I have already described how enhancement of the extinction of an aversion could be adaptive generally in allowing tamarins to track ecological change, but how is any benefit affected by the dynamics of the association between *S. fuscicollis* and *S. labiatus*? Well, it appears that it is not. No significant difference between species (i.e., averse *S. fuscicollis* interacting with non-averse *S. labiatus*, and averse *S. labiatus* interacting with non-averse *S. fuscicollis*) was found in the speed with which the extinction was overcome (i.e., the latency for each individual to consume their first piece of the preferred food) or in the subsequent consumption. So both species appeared to learn equally well from one another and therefore any benefit that may be accrued from overcoming an aversion as a result of interaction with others in a mixed-species troop would be symmetrical between species.

However, during the interactive condition, *S. labiatus* interacting with *S. fuscicollis* took more of the preferred food, once they had learned that it was in fact palatable, than did *S. fuscicollis* interacting with *S. labiatus*. This is likely to be due to the dominance of *S. labiatus* over *S. fuscicollis*. *S. labiatus* were observed to displace *S. fuscicollis* at the preferred food and monopolise it, once having re-established their preference for it through social learning.

So averse individuals of both species abandoned reliance upon information concerning the palatability of a preferred food gathered asocially in favour of information acquired from non-averse conspecifics and from congeners (although the subsequent exploitation of the food may be affected by the social dynamics between dyads). The lack of any difference in the general pattern of results for intra-specific and inter-specific interactants is perhaps surprising given that, as mentioned in the previous chapter, inter-specific interactions between associating tamarin species are rare in comparison to intra-specific ones (Pook & Pook, 1982; Norconk, 1986; Heymann, 1990a). However, no difference was found for species of demonstrator in Experiment 1 either. Again, this is possibly an indication of the considerable cohesion, integration and tolerance in mixed-species troops of tamarins in the wild and in captivity.

So, since averse individuals of both species are able to learn about the palatability of food from their non-averse conspecifics just as well as from their non-averse congeners, neither species are likely to gain a greater advantage from forming a large, single-species troop than forming a similarly-sized mixed-species troop. In fact, the opposite may be the case, in that, in a mixed-species troop, not only can individuals benefit from the knowledge of a large number of individuals (as is the case in a large single-species troop), but they can benefit from an increased knowledge base (i.e., the knowledge of their own species and any divergent knowledge their congeners might have).

6.8 Conclusion

For tamarins, membership in a cohesive social troop and performing most essential activities as a co-ordinated unit, would appear to provide a mechanism whereby essential information on food palatability can be efficiently transmitted between troop members.

When one member of a troop is feeding, the rest of the troop is generally feeding too, often in the same tree. Simply by virtue of belonging to a social troop, and doing what other members of the troop are doing, individuals are provided with the opportunity to learn what is palatable or safe to eat following a change in ecological conditions or for novel foods. Social learning in this way allows individuals to track environmental variability more efficiently than does asocial learning alone as social learners can quickly and safely home in on appropriate behaviour by sharing up to date foraging information (Laland *et al.*, 1993).

Since both the behaviour of congeners and conspecifics acts to influence food choice in a more adaptive direction, then mixed-species association will be advantageous in that the increased number of individuals in mixed-species troops increases the opportunity for information transfer accordingly. Moreover, although not supported here, mixed-species troops may be advantageous over similarly-sized single-species troops in that species can benefit from an increased knowledge base.

Chapter 7

Divergence in Forest Utilisation in Wild Troops of *S. fuscicollis* and *S. labiatus*

> *"Systematic comparison of the situations which do and those which do not release a given response - can be almost as good as planned experiments; the important thing it seems to me is not to miss the natural experiments and yet to know when it becomes necessary to continue by planned tests."*
>
> *[Tinbergen, 1958: p. 289]*

7.1 Introduction

The data presented in this chapter are that collected during three weeks of fieldwork carried out in the autumn of 1997. I was fortunate enough to join a research expedition in north-western Bolivia and this provided an opportunity to see my captive study subspecies, *S. fuscicollis weddelli* and *S. labiatus labiatus*, in the environment to which they are adapted. Observation of both the monkeys and their natural habitat had a profound influence on my appreciation of the nature of the problems faced by tamarins foraging in the wild, on my thinking regards the adaptivity of mixed-species tamarin troops, and on my understanding of the assumptions underlying the ecological validity of the experiments contained within this thesis. Being a member of the expedition team was an invaluable training exercise in how to conduct primatological fieldwork and also provided me with an opportunity to collect data for myself on some of the similarities and differences in the behaviour of *S. fuscicollis* and *S. labiatus* in their natural habitat. This information could then be used to identify some of the factors which permit association between these species. As described in Chapter 1, according to the Gause's (1934) principle of competitive exclusion, wherever two closely related species with strongly similar ecological requirements occur in sympatry, they enter into inter-specific competition which either drives one of the two species to local extinction or leads to character displacement. At first glance then, mixed-species tamarin troops would appear to contradict this principle. However, associating tamarin species exhibit divergence in several dimensions of their ecological niche which appears to permit their co-existence. For example, in this chapter, I present evidence for divergence in forest utilisation in wild mixed-species troops of *S. fuscicollis* and *S. labiatus*. I then relate these data to published data on niche divergence in the other tamarin association pairings to see how niche partitioning affects the stability of mixed-species tamarin troops. Finally, I compare data on forest utilisation (vertical segregation) for *S. fuscicollis* in associated troops to data for *S. fuscicollis* in non-associated troops, to see if differences in forest utilisation in mixed-species troops are a consequence of competitive displacement. Comparisons of the different tamarin association pairings with each other, and comparisons of data from associated troops with that from non-associated troops, act as natural experiments, helping to elucidate the relationship between niche partitioning and mixed-species troop formation and stability.

7.2 Method

7.2.1 Study Site

This study was conducted in the Pando Department, the youngest of Bolivia's departments, situated in the remote north-western corner of Bolivia and bordered by Brazil to the north and east, and Peru to the west (Figure 7.1). The study site is located near Rutina (11°24'S, 69°01'W), a timber sawmill on the Río Tahuamanu, south-west of the department capital, Cobija, and is best described as a mixture of primary and primary

Figure 7.1: Sketch map of South America showing the location of the Pando Department, Bolivia (shaded).

riverine forest (Figure 7.2). The distribution of *S. l. labiatus* is restricted to the area north of the Río Tahuamanu (Izawa & Bejarano, 1981; Rylands *et al.*, 1993), whereas *S. f. weddelli* has the widest distribution of the *S. fuscicollis* subspecies and occurs throughout the Pando Department (Hershkovitz, 1977; Izawa & Bejarano, 1981; Rylands *et al.*, 1993). Both species were encountered in the area, along with five other primate species: *Callimico goeldii* (Goeldi's monkey), *Callicebus brunneus* (brown titi monkey), *Cebus apella* (tufted capuchin), *Saimiri boliviensis* (Bolivian squirrel monkey), and *Pitheca irrorata* (Gray's bald-faced saki). *Alouatta sara* (Bolivian red howler monkey) were heard each morning, and *Aotus nigriceps* (night monkey) and *Cebus albifrons* (white-fronted capuchin) were reported to occur in the area.

7.2.2 Recording Methods

The data were collected by myself and Buchanan-Smith over a period of three weeks (between September and October, which coincides with the dry season). Either one or both of us would walk along observation trails or native paths, together with a guide, until we encountered primates. The observation trails had been cut for the purposes of the aforementioned expedition and the native paths cut by the indigenous peoples for rubber-tapping (*Hevea* spp.), Brazil nut (*Bertholletia excelsa*) collection or palm-tip (*Euterpe* spp.) collection (Cameron & Buchanan-Smith, 1992). The guide helped us locate primates by sight or hearing (he was particularly skilled at imitating the long call vocalisations of both *S. fuscicollis* and *S. labiatus*, to which they would begin antiphonal calling in reply).

Upon encountering a primate troop we would track it for as long as possible. Encounters ranged from a few minutes to follows of over 5 hours, and when the primates

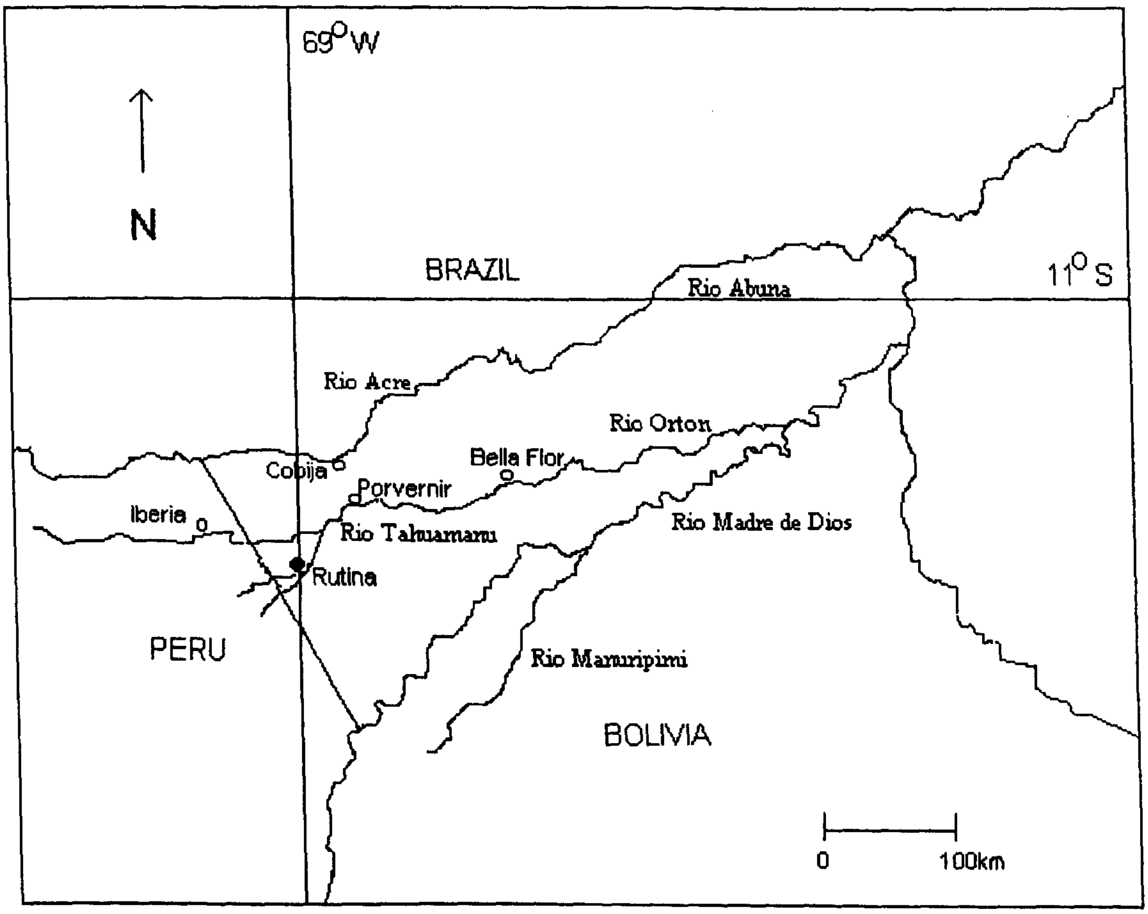


Figure 7.2: Sketch map of the Pando Department of north-western Bolivia with study site marked (•).

were visible we recorded data on a number of parameters. Where possible, estimates of troop size and the spread of individuals within the troop were made, and when two species were encountered together, the closest distance between individuals of the two species was also estimated. Species were recorded as being in proximity when both were visible to the observer simultaneously (usually within 20 - 40 m: the limit of visibility in the study area). Each observer collected data every 2 minutes on one individual of each species present by instantaneous scan sampling (Hinde, 1973). We ensured that we did not scan the same individual of each species, and we endeavoured to scan a different individual of each species on each consecutive scan. For each scan we recorded data on height in the forest (judged by eye and classified into 2 m categories for heights below 10 m, and 5 m categories for those above 10 m) and activity of the individual observed. Activity was classified into one of seven mutually exclusive categories in order to examine stratified use of the forest by activity. These were: locomotion, look (vigilance), insect forage (which includes insect feeding), fruit forage (which includes fruit feeding), groom, rest, and other (e.g., scent mark, scratch). Substrate orientation (horizontal = 1 - 15°, oblique = 16 - 74°, vertical = 75 - 90° deviations from the horizontal axis: see Garber, 1984a) and substrate size (small = < 5 cm diameter, medium = 5 - 10 cm diameter, large = > 10 cm diameter) were also recorded on each sample. In addition, leaps were recorded *ad libitum*.

7.2.3 Data Analysis

Primatologists in the field often experience difficulty in identifying distinct individuals. This is particularly difficult for those studying the Callitrichinae, due to their small size, lack of sexual dimorphism or sex-specific characteristics, and often timid nature. Consequently, it is rarely the case that the number of separate individuals in an encounter, and the number of times each individual has been observed, are known with certainty. Individual identification was not possible here. Nevertheless, it would be methodologically sound to perform statistical analyses on the first two data points collected by each individual on each encounter (thereby ensuring independence). However, due to the small number of encounters in the complete data set (n = 11 encounters), it was thought pertinent to present only descriptive statistics utilising all data points (n = 199 data points for *S. fuscicollis*; n = 359 data points for *S. labiatus*).

It is often the case that successive troops can be identified as independent due to the location in which they are encountered and to differences in their size and demography. Reliable troop identification was sometimes possible here. As a consequence of this, and due to difficulties experienced in estimating certain parameters, the sample sizes (number of encounters) given for certain estimates (e.g., troop size) are less than the total number of encounters.

To quantify vertical segregation I used Yoneda's (1984a) formula:

$$\mathrm{VS} = \sum_{i=1}^{5} |f_i - l_i|$$

where i indicates the types of forest layers, and f_i and l_i are the respective percentages of utilisation by *S. fuscicollis* and *S. labiatus* of forest layer *i*. For the purposes of this study these can be broken down into the forest floor (0 - 2 m), the lower layer (2 - 6 m), the lower-middle layer (6 - 10 m), the middle layer (10 - 20 m), and the upper layer (> 20 m) of the forest. The possible values of vertical segregation (VS) calculated from the formula range from 0 % (complete overlap between the species) to 200 % (complete segregation between the species).

7.3 Results

An indication of the occurrence of mixed-species troops of *S. fuscicollis* and *S. labiatus* within the population at Rutina was determined from the number of encounters during which each species was seen alone or in proximity with other primates at some point during the encounter. Table 7.1 shows the number of encounters during which *S. fuscicollis* were observed in proximity with other primates. *S. fuscicollis* were observed with other primates at some point during every encounter. The associating species was most often simply *S. labiatus* (n = 6). In the remaining encounters, *S. fuscicollis* were observed in tri-specific troops with *S. labiatus* and *P. irrorata* (n = 4), or occasionally *S. labiatus* and *C. brunneus* (n = 1).

Table 7.1: Number of encounters during which *S. fuscicollis* were observed in proximity with other primates at some point during the encounter.

***S. fuscicollis* in proximity with..**	**n**
S. labiatus	6
S. labiatus & *P. irrorata*	4
S. labiatus & *C. brunneus*	1

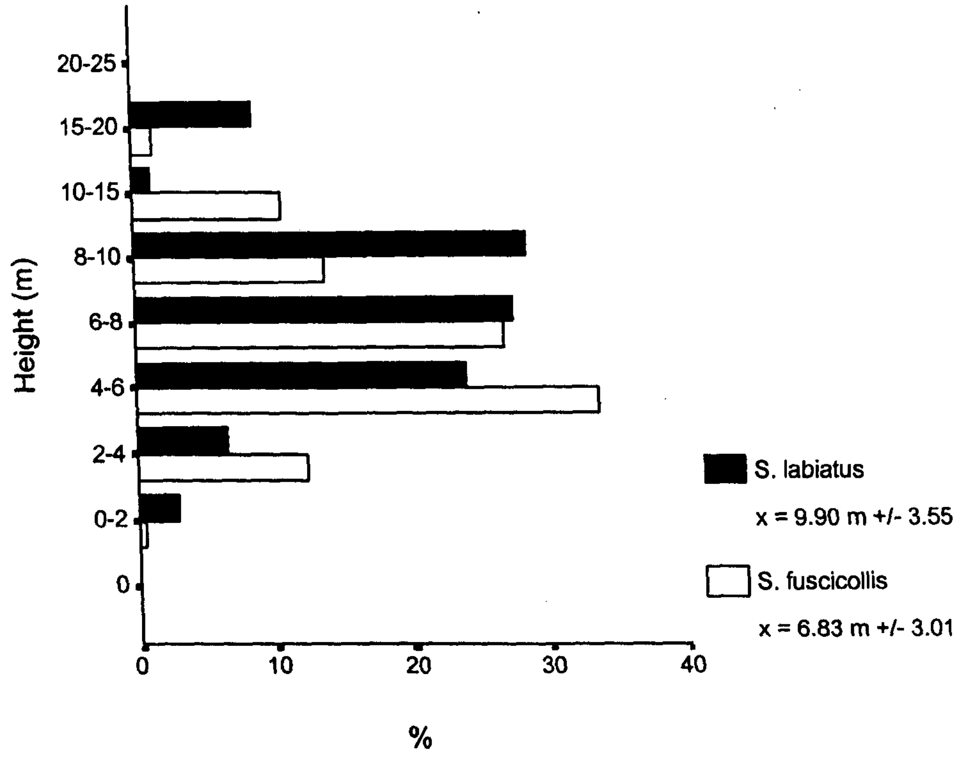
The modal and range of estimated troop sizes for *S. fuscicollis* and *S. labiatus* in these encounters are given in Table 7.2. *S. labiatus* was found to have a larger modal troop size than *S. fuscicollis*. Estimates of intra-specific and inter-specific troop spread were also made. The mean estimated intra-specific troop spread for *S. fuscicollis* was 22.00 m +/- 2.74 (SD; range 20 - 25 m, n = 5 encounters) and for *S. labiatus* was 27.14 m +/- 10.35 (SD; range 15 - 40 m, n = 7 encounters). Mean inter-specific troop spread between *S. fuscicollis* and *S. labiatus* was 13.89 m +/- 4.04 (SD; range 10 - 20 m, n = 11 encounters).

Table 7.2: Modal and range of estimated troop sizes for *S. fuscicollis* and *S. labiatus*.

Species	**Mode**	**Range**
S. fuscicollis (n = 6 encounters)	6	4 - 9
S. labiatus (n = 7 encounters)	8	5 - 13

Given such high frequencies of association, and a strong degree of cohesiveness, between these related species, it is of interest to compare the ecological niches occupied by them in order to see how similarities and differences in these permit their co-existence. Figure 7.3 shows the tamarin species' height utilisation in the forest. *S. labiatus* was generally found to use the higher height categories more so than *S. fuscicollis* which showed a preference for the lower height categories. *S. labiatus* showed considerably little activity at height category 10 - 15 m which is unusual. The mean height use in the forest for *S. fuscicollis* is 6.83 m +/- 3.01 (SD) and for *S. labiatus* is 9.90 m +/- 3.55 (SD) (means were calculated from the mid-point of each height category).

Figure 7.3: Comparison of height utilisation in the forest for *S. fuscicollis* and *S. labiatus*.



Using Yoneda's (1984a) formula, the vertical segregation (VS) between *S. fuscicollis* and *S. labiatus* is quantified at 56.8 %. This falls within the range of values given in other studies of *S. fuscicollis/S. labiatus* mixed-species troops (e.g., 47.3 % for primary forest, 76.9 % for secondary forest: Yoneda, 1984a; 65.5 %: Buchanan-Smith, 1999). Vertical segregation may lead to reduced feeding competition. Therefore it would be of interest to examine for differences in height use between the tamarins whilst they forage for their principal dietary components: insects and fruit. Table 7.3 shows the percentage of data points spent by the two species in each of the seven activity categories recorded. The main activities observed were locomotion and look (vigilance). This is likely to be due to the fact that the troops observed were not well habituated and sometimes fled from our presence. This did, however, make them more visible for data collection. Conversely, it is more difficult to observe the tamarins when they are resting.

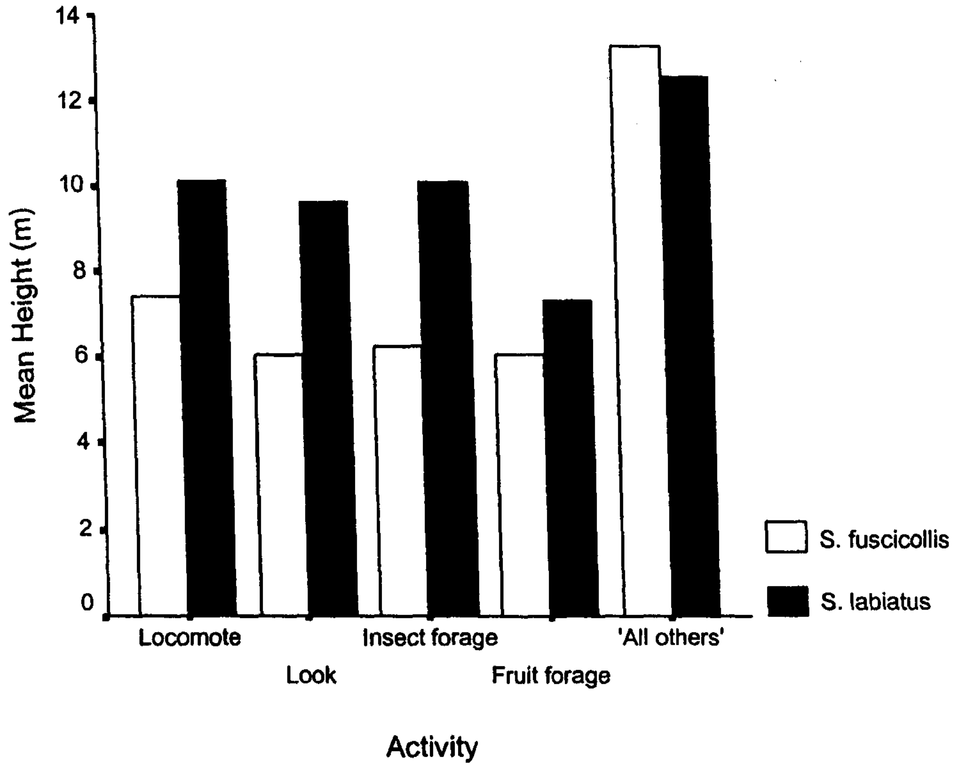
Unfortunately, the percentage of data points spent insect foraging and fruit foraging are so few as to preclude a detailed analysis of height differences whilst foraging.

Table 7.3: Percentage of data points spent in each of the seven activity categories for *S. fuscicollis* and *S. labiatus*.

Activity	***S. fuscicollis***	***S. labiatus***
Locomote	51.3	59.9
Look	28.2	25.4
Insect forage	4.5	3.3
Fruit forage	1.5	2.2
Groom	8.5	1.7
Rest	2.0	4.2
Other	4.0	3.3

Figure 7.4 shows the height utilisation in the forest for the different activity categories, collapsing groom, rest and other into one category called 'all others'. Differences between species in their vertical height in the forest were clearly manifest for the activities locomote, look and insect forage. There was little difference between the species in the heights at which they foraged for fruit or for the category 'all others'.

Figure 7.4: Comparison of height utilisation in the forest for different activities for *S. fuscicollis* and *S. labiatus*.



So *S. fuscicollis* were generally found to occupy a lower height in the forest than *S. labiatus*. In terms of the orientation and size of substrates utilised by the two species, *S. fuscicollis* is again clearly different from *S. labiatus* (Figures 7.5 and 7.6, respectively). *S. fuscicollis* used vertical substrates considerably more, and horizontal and oblique substrates less than *S. labiatus*. *S. fuscicollis* used large substrates more, and small substrates considerably less, than *S. labiatus*.

Figure 7.5: Comparison of orientation of substrates used by *S. fuscicollis* and *S. labiatus.*

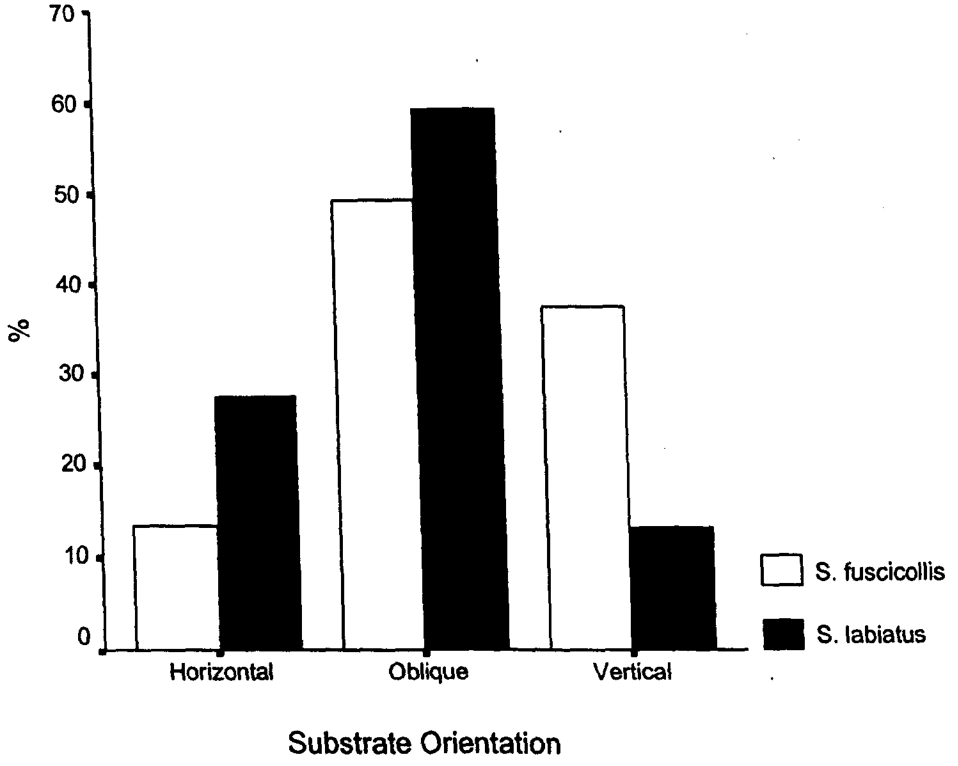
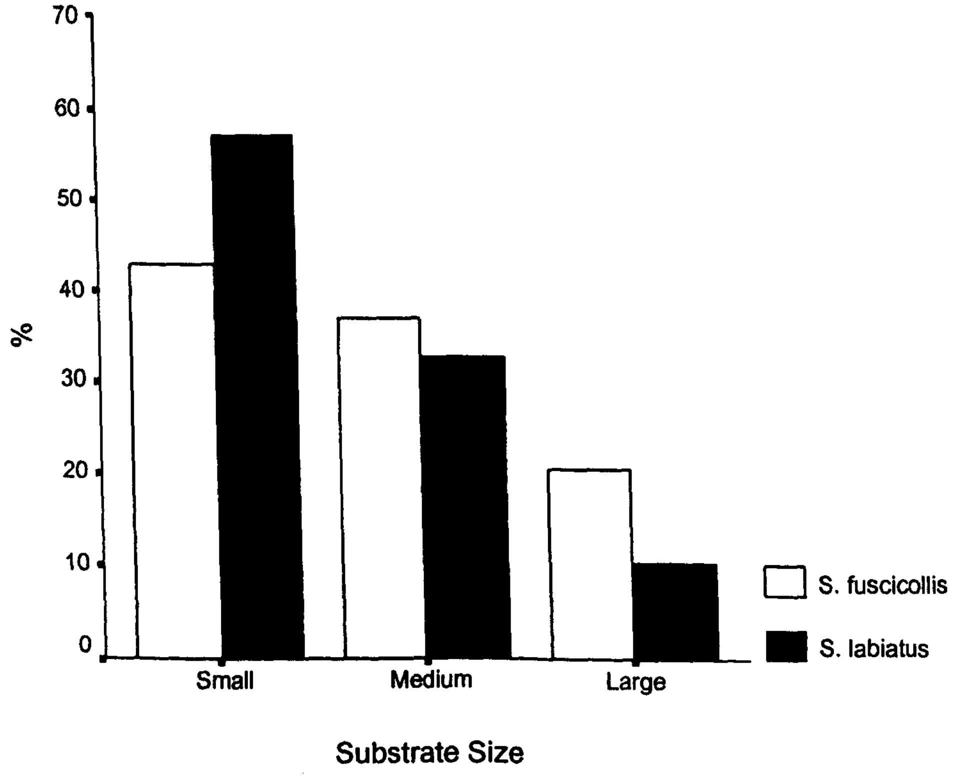
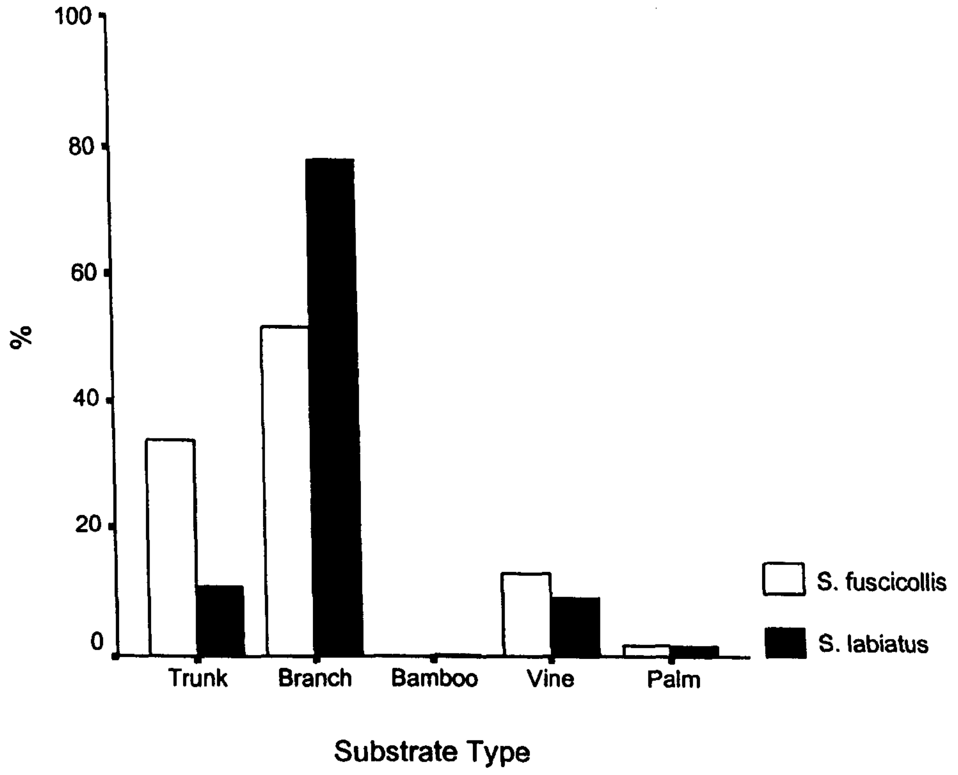


Figure 7.6: Comparison of size of substrates used by *S. fuscicollis* and *S. labiatus.*



The type of substrates used by the two species are shown in Figure 7.7. Both species made use of branches, trunks, vines, and rarely, palms. However, *S. fuscicollis* utilised considerably more trunks in their locomotion than did *S. labiatus*, whereas *S. labiatus* utilised considerably more branches in their locomotion than did *S. fuscicollis*.

Figure 7.7: Comparison of types of substrates used by *S. fuscicollis* and *S. labiatus*.



Overall, the data indicate that *S. fuscicollis* uses large, vertical substrates, which are generally tree trunks, more so than *S. labiatus*. *S. labiatus* uses small, horizontal and oblique substrates, which are generally branches, more so than *S. fuscicollis*. These differences in substrate size, orientation and type used by the two species are reflected in their means of progression through the forest. *S. fuscicollis* leaps mostly from trunk to trunk and branch to trunk (or vice versa) (more so than *S. labiatus*). *S. labiatus* leaps mostly from branch to branch (more so than *S. fuscicollis*) (Table 7.4).

Table 7.4: Percentage of branch to branch, branch to trunk (or vice-versa) and trunk to trunk leaps for *S. fuscicollis* and *S. labiatus*.

Leap Type	***S. fuscicollis*** **(n = 30 data points)**	***S. labiatus*** **(n = 59 data points)**
Trunk to trunk	56.7	5.1
Branch to trunk (or vice-versa)	33.3	22.0
Branch to branch	10.0	72.9

7.4 Discussion and Conclusion

In the past, the Pando Department of north-western Bolivia has been described as having one of the broadest spectra of primate species in South America (e.g., Izawa, 1979; Pook & Pook, 1982). In terms of primate species diversity, the study site at Rutina was found to be almost as rich as other more intensively studied areas in the Pando (Izawa & Bejarano, 1981; Pook & Pook, 1982; Cameron & Buchanan-Smith, 1992; Hardie, 1998; Buchanan-Smith *et al.*, in prep). In total, seven species were encountered in the area, another heard, and another two reported to occur there. *S. fuscicollis* and *S. labiatus* were encountered frequently and always in proximity with each other at some point during the encounter, that is, estimates of the frequency of encounter in mixed-species troops were 100 % for both species. These values are similar to the frequencies reported for these species by Hardie (1998) (88 % for *S. fuscicollis*; 83 % for *S. labiatus*), although estimates of the percentage of 'sightings' of mixed-species troops for *S. fuscicollis* and *S. labiatus* from the published literature range from 51 % to 93 % (see Table 7.5). (However, note that one problem in comparing frequencies of association for the different association pairings is that different authors use different criteria for 'in association': see Heymann & Buchanan-Smith, submitted). The mean estimated inter-specific troop spread between *S. fuscicollis* and *S. labiatus*, when compared to the values for intra-specific troop spread,

Table 7.5: Frequency of mixed-species tamarin troops reported in the existing literature (adapted from Heymann & Buchanan-Smith, submitted).

Associating Species	**% of Sightings or % of Troops**	**Reference**
Saguinus mystax mystax (with *Saguinus fuscicollis*)	58	Castro & Soini, 1978
	53	Glander *et al.*, 1984
	72	Heymann, 1990a
Saguinus labiatus labiatus (with *Saguinus fuscicollis*)	93	Christen & Geissmann, 1994
	83	Hardie, 1998
	64	Kohlhaas, 1989
	76	Pook & Pook, 1982
	70	Cameron *et al.*, 1989
	75	Buchanan-Smith, 1999
S. imperator subgrisescens (with *S. fuscicollis weddelli*)	59	Buchanan-Smith, 1999
Saguinus fuscicollis nigrifrons (with *Saguinus mystax*)	69	Glander *et al.*, 1984
	82	Heymann, 1990a
Saguinus fuscicollis weddelli (with *Saguinus labiatus*)	47	Christen & Geissmann, 1994
	88	Hardie, 1998
	51	Kohlhaas, 1989
	59	Pook & Pook, 1982
	57	Cameron *et al.*, 1989
	75	Buchanan-Smith, 1999
Saguinus fuscicollis weddelli (with *S. imperator*)	62	Buchanan-Smith, 1999
Saguinus fuscicollis weddelli (with *Callithrix emiliae*)	40	Martins *et al.*, 1987
Callimico goeldii (with *S. fuscicollis/S. labiatus*)	25	Cameron *et al.*, 1989
	44	Christen & Geissmann, 1994

indicates that the species were well integrated and moved (given that over half the data points were for locomoting) as a cohesive whole. It was difficult to obtain reliable counts of the number of individuals in the troops encountered. Nevertheless, the estimates of troop size in this study are comparable with those published previously. The modal troop size for *S. labiatus* was greater than that for *S. fuscicollis* which is in line with Freese *et al.* (1982), Hardie (1998) and Buchanan-Smith (1999), but in contrast with Yoneda (1981), Pook and Pook (1982), Buchanan-Smith (1990a) and Kohlhaas (1989)).

S. fuscicollis and *S. labiatus* were often encountered in proximity with a third species, either *Pitheca irrorata* or *Callicebus brunneus*. Observations of these tamarin species with *Pitheca* or *Callicebus* have been reported previously (e.g., Izawa & Bejarano, 1981; Pook & Pook, 1982; Buchanan-Smith, 1989, 1990b; Hardie, 1998), but these do not appear to be the co-ordinated, non-random and stable associations that characteristically occur between tamarin species. Instead, they seem to be limited to chance encounters at common food resources. (In this study, by far the most frequent activity recorded for *S. fuscicollis*, *S. labiatus* and either *Pitheca* or *Callicebus* in proximity was locomoting. Although, *S. fuscicollis* and *S. labiatus* were observed to fruit feed when in proximity with each other and *Pitheca*, and *S. labiatus* was observed to fruit feed when in proximity with *S. fuscicollis* and *Callicebus*, since *Pitheca* or *Callicebus* themselves were not observed to fruit feed in these instances no conclusions can be made regarding the exploitation of common resources).

According to accepted ecological theory, closely related species ought not to coexist without inter-specific competition leading to local extinction or character displacement (e.g., Schoener, 1988; Keddy, 1989). At first glance then, mixed-species tamarin associations would appear to contradict this principle. However, associating tamarin species exhibit divergence in several dimensions of their ecological niche which allows their coexistence. For example, from this study it is apparent that associating *S. fuscicollis* and *S. labiatus* utilise different locomotor styles, substrates, and heights in the forest. *S. fuscicollis* was found to occupy a lower mean height in the forest than *S. labiatus*. This pattern of vertical segregation is well documented in the published literature on the association between these species, although different absolute heights are reported due to local variants in forest type and height (e.g., Yoneda, 1981, 1984a; Pook & Pook, 1982; Buchanan-Smith, 1989, 1990a). The mean heights for both species in this study are rather low in comparison with the studies listed above. This is likely to be due to the relatively small number of data points in this study as well as to the particular forest type (mean height of the forest for the area north of the Río Tahuamanu is only 15.5 m: Buchanan-Smith *et al.*, in prep.). The mean height in the forest for *S. labiatus* in this study corresponds (roughly) with the lower forest canopy. The forest canopy is a horizontally continuous stratum made up of a network of limbs and branches of trees. Quadrapedal walking and running upon the branches of this network, or else leaping between them, is probably the most efficient method of locomotion for the substrates in this strata. Accordingly, the most frequent type of leaping observed for *S. labiatus* was from branch to branch. The mean height for *S. fuscicollis* was lower and corresponds with the forest understory. The forest understory, although connected vertically by foliage to the forest canopy, is discontinuous horizontally. The trees comprising it are smaller, and supports less stable, than those of the canopy. The most efficient means of progression from one part of the understory to another is via vertical clinging and leaping between vertical supports. In accordance with this, *S. fuscicollis* was most frequently observed leaping from trunk to trunk. These differences in locomotor behaviour are reflected in the data on the size and orientation of substrates used by the associating species. *S. fuscicollis* was found to use large-sized, vertically orientated substrates more so than *S. labiatus* (these were the trunks of trees in the forest understory). *S. labiatus* used small, horizontal and oblique substrates more so than *S. fuscicollis* (these were branches in the forest canopy). This divergence in forest utilisation is in line with the pattern observed for these species in other studies (e.g., Yoneda, 1981, 1984a; Pook & Pook, 1982; Hardie, 1998; Buchanan-Smith, 1999). A similar pattern is also reported for *S. fuscicollis* in association with *S. mystax* and with *S. imperator* (Norconk, 1990a; Garber, 1991; Smith, 1997; Buchanan-Smith, 1999).

So vertical segregation and locomotor behaviour are closely related, since arboreal progression through the forest at different heights requires different locomotor styles due to differences in the size, orientation and type of substrates in the separate strata. Both of these variables are also related to body size (Heymann, 1997), since positional behaviour is constrained by body size (Garber, 1992; Garber & Pruetz, 1995). Hence, the ability of *S. fuscicollis* to exploit their understory niche is largely due to their small size, which together with their 'claw-like' tegulae, allows them to vertically cling and leap between the vertical trunks found in the understory (although the tegulae are thought not have evolved as part of an adaptive complex for leaping, but simply as means of clinging to vertical supports: Kinzey *et al.*, 1975). Their congeners perform this method of locomotion much less frequently and this is probably due to constraints imposed by their larger size (Heymann, 1997). In fact, body size appears to be a critical factor generally in structuring communities, because it constrains not only positional behaviour but also diet, foraging techniques and strategies against predators (Charles-Dominique, 1977; Gautier-Hion, 1978;

MacKinnon & MacKinnon, 1980; Struhsaker, 1978; Terborgh, 1983). For example, also by virtue of their small size and by embedding their tegulae into the bark of trees, *S. fuscicollis* are able to adopt a stable posture from which to explore knotholes, crevices and other regions of the trunk in order to locate their bark-refuging insect prey (Terborgh, 1983, 1985; Yoneda, 1984a,b; Garber, 1992; Buchanan-Smith, 1990a; Peres, 1992b; Heymann, 1990a). The larger *S. labiatus* are less well adapted to the understory and are found to forage for their insect prey higher up in the forest canopy (Yoneda, 1981, 1984a; Pook & Pook, 1982; Buchanan-Smith, 1989, 1990a; Hardie, 1998). They glean more mobile prey from the foliage and branches of the canopy using a more dynamic stalk and pounce technique (Yoneda, 1981, 1984a; Garber, 1993a). The use of the same strata and substrates during insect foraging would mean that the same micro-habitats are searched for prey, resulting in a high overlap in the spectrum of animal prey captured. Since animal prey represents the highest quality dietary component of wild tamarins, vertical segregation during insect foraging (as a result of adaptation to separate strata), leading to resource partitioning, may be critical for the formation of mixed-species tamarin troops (Heymann, 1997). That is, divergence in insect foraging may reduce the overall potential for inter-specific food competition and allow the species to co-exist amicably.

In summary then, vertical segregation between associating species in wild mixed-species tamarin troops is primarily a consequence of the ecological, behavioural and related morphological adaptations which orient these monkeys towards particular strata and the specific microhabitats were their principal animal dietary components are found. These adaptations allow co-existence in mixed-species troops.

Confirmation of the importance of vertical segregation for mixed-species tamarin troops come from comparisons across the three tamarin association pairings (Buchanan-Smith, 1999). Comparing data on *S. fuscicollis/S. labiatus* troops and *S. fuscicollis/S. imperator* troops, together with published data for *S. fuscicollis/S. mystax* troops (Norconk, 1990b), Buchanan-Smith found that the degree of vertical segregation between associating species is least for *S. fuscicollis/S. imperator* troops and greatest for *S. fuscicollis/S. mystax* troops, whilst that for *S. fuscicollis/S. labiatus* troops is intermediate. Now, comparing this finding with data on the stability of the different tamarin associations, again from published literature (see Table 7.5 and Table 1.1), it is found that the degree of association between the three tamarin association pairings is positively correlated with increasing vertical segregation, it being least in *S. fuscicollis/S. imperator* troops and greatest in *S. fuscicollis/S. mystax* troops (Figure 7.8). This suggests that vertical segregation may play a significant role in mixed-species troop formation in tamarins as has been proposed for the ecology of other related sympatric primate species (e.g., Charles-Dominique, 1977; Gautier-Hion, 1978; Struhsaker & Oates, 1979; Fleagle, 1980; MacKinnon & MacKinnon, 1980; Richard, 1985; Ungar, 1996).

Figure 7.8: Trends in tamarin mixed-species associations.

	Association Pairing		
	S. fuscicollis / S. imperator	***S. fuscicollis/ S. labiatus***	***S .fuscicollis/ S. mystax***
Permanency and Stability (Degree of Association)	——————————————————→		
Vertical Segregation	——————————————————→		
Body Size Ratios	——————————————————→		
Dietary Overlap (Fruit)	——————————————————→		
Differences in Insect Foraging Strategies		High for all	

The pattern for vertical segregation appears to fit with patterns observed in other aspects of ecological niche differentiation in associations between *S. fuscicollis* and the members of the *S. mystax* group (Figure 7.8). For example, Heymann (1997) has related the stability of associations to body-size ratios; the difference between *S. fuscicollis* and *S. imperator* is smallest, and that between *S. fuscicollis* and *S. mystax* largest. As described earlier, body size has a pervasive impact on ecology and behaviour and, as such, can influence stability of association. Heymann also discusses the relationship between association patterns and dietary overlap. Dietary overlap is greatest for *S. fuscicollis* and *S. mystax* (80 - 85 %: Norconk, 1986; Castro, 1991; Peres, 1993b) and lowest for *S. fuscicollis* and *S. imperator* (43 %: Terborgh, 1983). This could lead to a reduction in the stability of the association for *S. fuscicollis* and *S. imperator* by decreasing their opportunity to feed on fruit together, as has been suggested for *Cercopithecus ascanius* (red-tailed monkey) and *Cercopithecus mitis* (blue monkey) at Kibale compared to Kakemaga (East Africa) (Cords, 1990).

So vertical segregation, combined with differences in body size and dietary overlap, plays an important role in tamarin mixed-species troop formation. Given its importance, might not vertical segregation play a role in tamarin mixed-species troops in other ways, apart from leading to resource partitioning for insect prey? Buchanan-Smith (1999) and Heymann and Buchanan-Smith (submitted) suggest that it might by increasing the potential for both the anti-predatory benefits and foraging benefits accrued to mixed-species troops. These benefits are not necessarily mutually exclusive because, for most associating tamarin species, there is extensive dietary overlap between them allowing close association (and therefore the potential to benefit from each other's vigilance behaviour) as they travel to shared feeding sites (Terborgh, 1983). Instances in which only one class of benefits applies are thus likely to be rare, but let us for a moment consider each in isolation.

Associating but vertically segregated species might increase their overall anti-predatory benefit by virtue of being better placed to detect predators in the whole of their environment due to the complementary nature of the vigilance behaviour of each species at different heights in the forest. For example, Peres (1993a) reports that *S. fuscicollis* are more vigilant at lower levels of the forest, perform more downward scanning, and detect more terrestrial and scansorial threats than their congeners. *S. mystax* are more vigilant at higher levels, perform more sideways and upward scans, and detect more aerial and arboreal threats. Support for this proposition generally, comes from primate associations where there is no dietary overlap between associating species (and thus foraging benefits are precluded) yet vertical segregation is still apparent (Oates & Whitesides, 1980, for *Procolobus versus* (olive colobus) and cercopithecine species; Bshary & Noe, 1997; Wachter *et al.*, 1997, for *Colobus badius* (red colobus) and *Cercopithecus diana* (Diana monkey)).

Vertical segregation could increase the potential for two of the foraging benefits proposed for mixed-species tamarin troops: (1) increased prey capture rates, and (2) increased detection and knowledge about resources at different heights. Peres (1992b) has described *S. mystax* flushing insects (large orthopterans) to lower levels in the forest which facilitates their capture by *S. fuscicollis*. Since animal prey represents the highest quality dietary component of wild tamarins, the opportunity to exploit such prey may be a major incentive for *S. fuscicollis* to associate. Peres (1996) has also provided evidence relating to the second foraging benefit to be improved through vertical segregation. *S. mystax* are more often the first to encounter large productive feeding patches located higher in the forest (trees that can accommodate the whole mixed-species troop), whereas *S. fuscicollis* are more often the first to encounter smaller food patches lower in the forest, from which they are often displaced by the dominant *S. mystax*. The opportunity to exploit each other's food finds at different heights may increase overall foraging efficiency.

It has been proposed also that vertical segregation may ameliorate the intensity of inter-specific competition by acting to decrease the frequency of competitive interactions in mixed-species troops (Buchanan-Smith, 1999; Heymann & Buchanan-Smith, submitted). If vertical segregation between associating species is a consequence of displacement due to competition, then it follows that the range of heights used by *S. fuscicollis* should be different in the absence of their dominant congeners. One would expect *S. fuscicollis* to be displaced to a lower vertical height from being in association with their dominant congeners, for whom no such shift is expected. However, this suggestion finds no support. This study and those by Yoneda (1984a), Buchanan-Smith (1990a, 1999) and Hardie (1998) found *S. fuscicollis* to reside predominantly in the 0 - 10 metre area of the forest when in association with *S. labiatus*. These findings for height utilisation in the forest are similar to those reported for *S. fuscicollis* in single-species troops. For example, Buchanan-Smith (1999) reports that, in the absence of other tamarins, 99 % of *S. fuscicollis* records were below 15 metres and the mean height was not significantly less than at sites with congeneric tamarins. Similarly, Soini (1987) found that in single-species troops of *S. fuscicollis illigeri* (Illiger's saddle-backed tamarin), 82 % of daytime records were below 11 metres and 50 % below 4 metres. It appears that *S. fuscicollis* do not differ in height use in and out of association, and thus it seems unlikely that the pattern of vertical segregation in associating species is a consequence of competitive displacement (Buchanan-Smith, 1999). However, this comparison was made using overall height use in the forest (i.e., for all behavioural activities) in and out of association. What one ought to do is compare height differences *whilst foraging*, and not just overall heights. Such a comparison was not possible in this study due to the small number of data points for foraging and the fact that the species were always found in association.

Although data points for foraging were few in this study, *S. fuscicollis* were found to forage for insects at a lower mean height than *S. labiatus*. This finding is in accordance with the published literature for these species (Yoneda, 1981, 1984a; Pook & Pook, 1982; Buchanan-Smith, 1989, 1990a, 1999; Hardie, 1998). The species in this study did not differ in their heights for fruit foraging. This finding is also consistent with published literature on vertical segregation during fruit foraging for these species (Yoneda, 1981; Buchanan-Smith, 1990a, 1999; Hardie, 1998). There is considerable overlap in the plant component of the diet of these species (62.5 %: Hardie, 1998), as there is for *S. fuscicollis* and *S. mystax* (80 - 85 %: Norconk, 1986; Castro, 1991; Peres, 1993b, 1996), and *S. fuscicollis* and *S. imperator* (43 %: Terborgh, 1983). (Although, note that different authors have used different methods for quantifying dietary overlap: see Heymann & Buchanan-Smith, submitted). Thus they are usually found to fruit forage at the same height, and sometimes in the same tree. This, together with a general lack of inter-specific aggression (and no increase in competition or ranging with increases in the size of mixed-species troops), has led researchers to conclude that fruit is generally not limiting for mixed-species troops of tamarins (Garber, 1988b), although during the dry season when overall fruit production is low (Janson *et al.*, 1981) it probably is.

To conclude, it appears that, in order to limit the negative effect of inter-specific competition on troop stability and cohesion, associating tamarin species have evolved behavioural and morphological specialisations to separate strata that consequently permit co-existence. For example, despite consuming very similar plant based diets (e.g., Terborgh, 1983; Garber, 1988b, 1993a; Peres, 1993b), associating tamarin species are characterised by different prey foraging techniques and exploit different types of invertebrate prey (Nickle & Heymann, 1996). These adaptations, together with differences in body size, also allow co-existence in mixed-species troops by increasing the potential for other advantages accrued to mixed-species troops through vertical segregation (e.g., decreased predation risk; increased probability of detecting food resources), and possibly by reducing inter-specific feeding competition. However, although associating tamarin species segregate themselves vertically during insect foraging, it is not evident from the available field literature whether this is simply a consequence of adaptation to the specific strata in which their particular insect prey are found, or whether the observed vertical segregation is also due, in some part, to competitive displacement or to a simple change in height preference when associated. That is, we know very little about exactly what effect the presence of a congener has on height use during foraging. For example, do *S. fuscicollis* choose to insect forage at lower heights in the presence of *S. labiatus* because it is beneficial for them to do so, or because they are forced to do so by *S. labiatus*. Conversely, do *S. labiatus* choose to confine their insect foraging to higher heights in the presence of *S. fuscicollis* or are they displaced upwards by them. As mentioned earlier, what one ought to do to examine this issue is to compare height use during insect foraging whilst in and out of association. However, because, in areas of sympatry, associating species are most often found in association, these data are rarely available from the wild. It is, of course, possible to compare wild mixed-species troops with wild single-species troops from different study sites, but such comparisons are confounded by differences in variables between sites (such as habitat type, home range size, food availability and predation pressure). In captivity, it is possible to study the same individuals in single-species troops and in mixed-species troops to see directly what effect the presence of a congener has on behaviour. Therefore, to further explore the issue of vertical segregation leading to reduced inter-specific feeding competition, experiments were conducted in captivity with foraging boxes presented at two different heights. These are presented in the following chapter.

Chapter 8

Foraging Height Preferences and Inter-Specific Feeding Competition in Captivity

"Every species has its niche, its place in the grand scheme of things."

[Colinvaux, 1978: p. 10]

8.1 Introduction

Competition theory predicts that, under resource-limited conditions, associated heterospecifics should segregate ecologically to a certain degree, or else their long-term existence could be threatened by competitive exclusion (e.g., May, 1973). While differences in diet and feeding behaviour are clearly critical to niche partitioning, synecologists consider stratigraphic segregation in the forest also to be an important method by which sympatric and associated primates partition their niches (e.g., Charles-Dominique, 1977; Gautier-Hion, 1978; Struhsaker & Oates, 1979; Fleagle, 1980; MacKinnon & MacKinnon, 1980; Terborgh, 1983; Richard, 1985; Ungar, 1996). Vertical segregation has been observed in all wild tamarin mixed-species troops which have been studied in detail. All, including this study, report *S. fuscicollis* occupying a lower stratum than its congeners (*S. labiatus*: Yoneda, 1981, 1984a; Pook & Pook, 1982; Buchanan-Smith, 1990a, 1999; Hardie, 1998; *S. mystax*: Peres, 1991; *S. imperator*: Terborgh, 1983; Buchanan-Smith, 1999). In the previous chapter, it was suggested that vertical segregation may play an important role in mixed-species troop formation in tamarins by reducing inter-specific feeding competition. To examine the relationship between vertical segregation and inter-specific feeding competition, a series of experiments were conducted in captivity with

S. fuscicollis and *S. labiatus*. Vertical segregation has been observed previously in captive mixed-species troops of these species (Hardie *et al.*, 1993; Hardie, 1995; McShane, 1995). For example, Hardie found that *S. fuscicollis* individuals occupied a lower mean height in their enclosures than did *S. labiatus* individuals. Given these findings, it is reasonable to expect that each species might exhibit foraging height preferences in captivity. In Experiment 4, foraging boxes containing one of two different quantities of food were presented at one of two different heights to single- and mixed-species troops and the foraging behaviour and competitive interactions of individuals at the foraging boxes recorded. Data analysis allowed me to determine if the species exhibited foraging height preferences, and by comparing single-species troops with mixed-species troops, whether these preferences were altered by the presence of a congener. As described in Chapter 2 (Section 2.2.1), *S. labiatus* are larger than, and dominant to, *S. fuscicollis* and, in the wild, can and do displace them at feeding sites (Buchanan-Smith, 1989; Hardie, 1998). Given this dominance relationship between the species, one might expect *S. fuscicollis* to be displaced from their preferred foraging height if that is the height that *S. labiatus* also prefer.

8.2 Experiment 4: Foraging Height Preferences and Feeding Competition (One Box Present)

The aims of the experiment were to determine if single-species pairs of S. fuscicollis *and* S. labiatus *exhibit foraging height preferences; and to determine whether, in mixed-species troops, these preferences are altered by the presence of a congeneric pair.*

8.2.1 Study Animals

The study animals were seven troops of *S. fuscicollis* (SF1, SF3, SF4, SF5, SF6: Table 4.1; SF9, SF11: Table 4.3) and seven troops of *S. labiatus* (SL1, SL2, SL4, SL5, SL6: Table 4.2; SL7, SL11: Table 4.4) housed in the separate indoor/outdoor enclosures in the 'Old Marmoset-House'. Further details of housing and husbandry are given in Chapter 4 (Section 4.6). Normally maintained as mixed-species troops, the monkeys were tested as either single-species troops (SF1, SL1) or as both single-species troops and mixed-species troops (SF3 & SL2, SF4 & SL4, SF5 & SL5, SF6 & SL6, SF9 & SL7, SF11 & SL11). All troops consisted of an adult male-female pair together with any dependent offspring, of which only the adult pair were tested. SF1 and SL1 were an exception to this. Both consisted of an adult male-female pair and their sub-adult son and daughter, all of which were tested. Being twice the size of the other single-species troops but the same size as the mixed-species troops, comparing the data from SF1 and SL1 with that of the mixed-species troops acted as a control for troop size effects.

8.2.2 Design

The experiment was designed so that height preferences could be investigated in the absence of a congener (single-species troops) and in the presence of a congener (mixed-species troops). Each troop received four separate test trials as a single-species troop and four as a mixed-species troop, during which one foraging box containing one of two possible quantities of food was presented to them at one of two possible heights. The foraging box was a semi-transparent polypropylene container measuring approximately 13 cm x 8 cm x 6 cm and patterned with one of two different designs (vertical stripes or filled-circles) (Plate 11). The designs were used to indicate that the box contained one of two

Plate 11: *S. labiatus* utilising a foraging box

possible quantities of food (mealworms concealed beneath a 3 cm layer of sterile wood shavings). The monkeys were trained to associate a particular design with a particular quantity of hidden food. (This was necessary for Experiment 5 which investigated whether preferred foraging height would be traded-off against food quantity. Food quantity was not analysed in this experiment). The designs were assumed to be equally visible and were counterbalanced to eliminate preference effects (i.e., for half the troops, vertical stripes indicated five food items, and filled-circles, twenty food items; and for the other half the reverse). The foraging box was fixed to a large (>10 cm in diameter), horizontal branch at either 50 cm or 150 cm from the ground, according to test condition. Average height use in the enclosure was approximately 125 cm from the ground for both species. The four trials were the four possible combinations of food quantity and height (i.e., five food items at 50 cm; twenty food items at 50 cm; five food items at 150 cm; twenty food items at 150 cm). The order of trial presentation was counterbalanced across troops to control for order effects. Also, to control for order effects, half the troops were tested as single-species troops first and mixed-species troops second and the other half the reverse. All mixed-species troops had been mixed prior to experimentation and thus those receiving the single-species testing first required only two days habituation to their congeners and their enclosures upon re-mixing for the mixed-species testing.

McShane (1995) and Hardie (1995) have shown that the insect foraging patterns of the tamarins at Belfast Zoological Gardens are comparable to those of their wild counterparts. The insect foraging technique of *S. fuscicollis* is primarily extractive with occasional opportunistic attempts at catching dipteran species as they fly past, whereas *S. labiatus* adopts a seize and capture approach after hunting or stalking dipteran prey from under leaves and on branches. Since I was unable to use mobile insect prey as experimental food items, because I needed to control the distribution of the food items carefully, I used relatively sedentary mealworms contained within the boxes and concealed beneath wood shavings. I was a little apprehensive that the extractive nature of the foraging task would make it more suited to the primarily extractive-foraging *S. fuscicollis*. However, the *S. labiatus* exhibited no difficulty in searching within the boxes for the mealworms and learned to do so as quickly as did the *S. fuscicollis*. The experiment was conducted between May and September, 1996, and between May and August, 1997.

8.2.3 Procedure

Pre-training, training and test trials were conducted before the monkeys' daily feed to ensure they were motivated to search for the food items. The experimental procedure was as follows:

(1) *Pre-training Trials*

The monkeys received a basic pre-training to ensure they were familiar with foraging for food items from the boxes before training to the significance of the designs began. A mixed-species troop was moved to the 'End-Enclosure' and the two species each allowed to occupy one of the separate enclosures, C10 and C11, the outdoor portions of which adjoined the 'End-Enclosure' (see Figure 4.1). If the two species were to be tested as single-species troops first, then they could be released alternately from their respective enclosures into the 'End-Enclosure' for testing. If they were to be tested as mixed-species troops first, then they could be contained in either C10 or C11 immediately before release into the 'End-Enclosure' in order that they may be released simultaneously.

Following two days habituation to their new enclosures and to the 'End-Enclosure', each troop was presented, on a daily basis, with twelve food items inside an unmarked foraging box, without foraging material (wood shavings), in the indoor area of their enclosure, in order to habituate them to the apparatus. The box was positioned on the resting/sleeping shelf in the indoor portion of the enclosure, approximately 125 cm from the floor. Presentations continued until it was observed that every member of each troop would readily approach the box and forage for the food items contained within it. Once this was established, twelve food items were again presented in the box, but this time concealed beneath a 3 cm layer of wood shavings. Again presentations continued until all individuals were familiar with foraging for the food items in this manner. Pre-training and training trials were necessary only for those troops unfamiliar with taking food items from the boxes and were thus only received once, at the commencement of the experiment, whether the troops were to be tested as single-species troops first or as mixed-species troops first.

(2) *Training Trials*

Following pre-training, the monkeys received five consecutive days of training trials, two per day for each troop (one in the morning and one in the afternoon) in order that they might learn that the different designs on the foraging boxes signified different quantities of food. This was done in the indoor portion of the monkeys' enclosures. Species were trained separately, regardless of whether they were to be tested as single-species troops or as mixed-species troops first. Training in the indoor area ensured that there would be no positional biases present during testing in the 'End-Enclosure'. Once again, the training box was positioned on the shelf in the indoor portion of the enclosure. Five and twenty food items were presented, concealed under a 3 cm layer of wood shavings, in the appropriately patterned box. The order of box presentation (i.e., five food items presented in the morning, twenty food items presented in the afternoon; or vice-versa) was counterbalanced between troops to avoid order effects. Half the study troops were trained to recognise that the box with the vertical stripes design contained five food items and that that with the filled-circles design contained twenty food items. For the remaining troops, this was reversed to act as a control to test for pattern preference. No data were collected during training.

(3) *Test Trials*

Test trials were conducted in the 'End-Enclosure'. Each single-species troop and mixed-species troop received four test trials as described in Section 8.2.2, two per day, commencing the day after training was completed. Immediately before testing, the single-species troops to be tested were shut into the indoor area of their respective enclosures (C10 and C11) whilst the appropriate quantity of food was placed in the appropriate box (secured on branches at the appropriate heights in the 'End-Enclosure') and concealed under a 3 cm layer of wood shavings. For the mixed-species troops, both species were shut into one of their respective enclosures. Recording began approximately 1 minute later, at the moment the connecting door between the enclosure and the 'End-Enclosure' was opened (from the outside via a wire pulley) and the monkeys were free to enter the 'End-Enclosure' to forage. Recording continued for a period of 20 minutes, or until all the food items were thought to have been consumed and no monkey had approached within 15 cm of either box for over 5 minutes.

8.2.4 Recording Methods

A miniature tape recorder was used to dictate a verbal record of all instances in which an individual approached within 15 cm of the box, touched the box, searched through the wood shavings (i.e., actively manipulated them, raking them, cupping them or flicking them out of the box, in order to see if a mealworm was concealed beneath them), obtained a food item, and exited outwith 15 cm of the box (all-occurrences behavioural sampling: Altmann, 1974). In addition, I noted any competitive interactions (food stealing, agonistic behaviour and displacements: see Table 4.5), along with the context and identity of the individuals involved (actor/s and receiver/s). Finally, any calls (alarm, food or other) were recorded. (However, data on calls are not presented because of the difficulty experienced in confirming the identity of the caller at such a localised food source). Data were subsequently transcribed from audio-tape onto record sheets. Playback, synchronised with an electronic stopwatch, enabled a note to be made of the time at which each of the behaviours dictated into the tape recorder were performed.

8.2.5 Data Analysis

From the data collected, it was possible to derive latencies (in seconds), from entering the 'End-Enclosure', for each individual in each trial to: (a) approach the box (i.e., within 15 cm of the box); (b) touch the box; and (c) obtain their first food item. There was found to be little difference in the pattern of latencies to perform these behaviours, so only data for the latency for each monkey to obtain their first food item will be presented. It was also possible to calculate for each individual: (e) their total duration spent within 15 cm of the box; (f) the number of searches performed; and (g) the number of food items eaten. Of these variables, only the data on duration will be presented here, and only for single-species troops.

Statistical comparisons between heights or condition (single-species or mixed-species testing) were made using the Wilcoxon Signed-Ranks test. Comparisons between species were made using the Mann-Whitney U test. Non-parametric statistical tests were used because of sample-size limitations ($n = 12$ pairs for the tables that follow) and deviations from normality. Significance was set at alpha < 0.05. Data on the direction and total frequency of competitive interactions are also presented.

8.3 Results

Single-species Troops

Considering the latency data first, in single-species troops of two individuals, *S. fuscicollis* were significantly faster to obtain a food item from the box with five food items when it was presented at 150 cm from the ground than at 50 cm from the ground (Table 8.1). They exhibited no significant difference in their latency to obtain a food item from the box with twenty food items. *S. labiatus* were significantly faster to obtain a food item from the box with five food items and that with twenty food items when these were presented at 150 cm from the ground than at 50 cm from the ground.

Table 8.1: Median latencies (seconds) to obtain a food item from boxes with five and twenty food items at 150 cm and 50 cm from the ground for *S. fuscicollis* and *S. labiatus* in single-species troops.

Species	**Quantity**	**150 cm**	**50 cm**	**Z value**
S. fuscicollis	5 items	30.5	66.0	$z = -2.04$, $\mathbf{p < 0.05}$
S. fuscicollis	20 items	38.5	65.5	$z = -1.65$, $p > 0.05$
S. labiatus	5 items	49.5	93.5	$z = -2.04$, $\mathbf{p < 0.05}$
S. labiatus	20 items	23.5	100.0	$z = -2.93$, $\mathbf{p < 0.05}$

P-values refer to Wilcoxon Signed-Ranks test. Bold indicates a significant result.

Using the same data but re-arranging to show species differences, there was no species difference in the latency to obtain a food item from the box with five food items at 150 cm from the ground (Table 8.2). *S. labiatus* were found to be significantly faster than *S. fuscicollis* to obtain a food item from the box with twenty food items at 150 cm from the ground. *S. fuscicollis* were significantly faster than *S. labiatus* to obtain a food item from the box with five food items and that with twenty food items at 50 cm from the ground.

Table 8.2: Species differences in median latencies (seconds) to obtain a food item from boxes with five and twenty food items at 150 cm and 50 cm from the ground in single-species troops.

Height	**Quantity**	***S. fuscicollis***	***S. labiatus***	**Z value**
150 cm	5 items	30.5	49.5	$z = -1.33$, $p > 0.05$
150 cm	20 items	38.5	23.5	$z = -2.66$, $\mathbf{p < 0.05}$
50 cm	5 items	66.0	93.5	$z = -2.60$, $\mathbf{p < 0.05}$
50 cm	20 items	65.5	100.0	$z = -2.16$, $\mathbf{p < 0.05}$

P-values refer to Mann-Whitney U test. Bold indicates a significant result.

Now considering the duration data, there was a trend for both species to spend longer within 15 cm of the box when it was presented at 150 cm from the ground than at 50 cm from the ground, regardless of the number of items it contained (Table 8.3). However, this trend was only statistically significant for *S. fuscicollis* when the box contained 20 items and for *S. labiatus* when the box contained 5 items.

Table 8.3: Median durations (seconds) spent within 15cm of the boxes with five and twenty food items at 150 cm and 50 cm from the ground for *S. fuscicollis* and *S. labiatus* in single-species troops.

Species	**Quantity**	**150 cm**	**50 cm**	**Z value**
S. fuscicollis	5 items	90.5	80.0	$z = -0.31$, $p > 0.05$
S. fuscicollis	20 items	198.5	140.0	$z = -2.20$, $\mathbf{p < 0.05}$
S. labiatus	5 items	110.5	62.0	$z = -2.69$, $\mathbf{p < 0.05}$
S. labiatus	20 items	197.5	129.0	$z = -1.57$, $p > 0.05$

P-values refer to Wilcoxon Signed-Ranks test. Bold indicates a significant result.

Using the same data but re-arranging to show species differences, there were no species differences in duration spent within 15 cm of any of the boxes (Table 8.4).

Table 8.4: Species differences in median durations (seconds) spent within 15 cm of the boxes with five and twenty food items at 150 cm and 50 cm from the ground in single-species troops.

Height	**Quantity**	***S. fuscicollis***	***S. labiatus***	**Z value**
150 cm	5 items	90.5	110.5	$z = -0.87$, $p > 0.05$
150 cm	20 items	198.5	197.5	$z = -0.66$, $p > 0.05$
50 cm	5 items	80.0	62.0	$z = -0.87$, $p > 0.05$
50 cm	20 items	140.0	129.0	$z = -0.03$, $p > 0.05$

P-values refer to Mann-Whitney U test. Bold indicates a significant result.

In view of the results presented thus far, *S. labiatus* appear to have a preference for the upper box. That is, they showed a reduced latency to this box compared to the lower box, were faster than the *S. fuscicollis* to this box when it contained twenty food items, and spent longer within 15 cm of this box compared to the lower box when it contained five food items. *S. fuscicollis* show a less-clear preference for the upper box. That is, they were faster to this box compared to the lower box only when it contained five food items and spent longer within 15 cm of this box compared to the lower box only when it contained twenty food items. *S. fuscicollis* were, however, faster than *S. labiatus* to the lower box when it contained five food items and when it contained twenty food items.

Mixed-species Troops

How are these preferences altered in mixed-species troops? *S. fuscicollis* in mixed-species troops, as in single-species troops, exhibited no significant difference in their latency to obtain a food item from a box with twenty food items presented at 150 cm from the ground than at 50cm from the ground (Table 8.5). Nor did they exhibit a significant difference in their latency to obtain a food item from the box with five food items. *S. labiatus* were significantly faster to obtain a food item from the box with five items when it was presented at 150 cm from the ground than at 50 cm. There was a similar but non-significant trend for the box with twenty items. Thus in mixed-species troops, the preference of *S. labiatus* for the upper box appears largely unchanged.

Table 8.5: Median latencies (seconds) to obtain food item from boxes with five and twenty food items at 150 cm and 50 cm for *S. fuscicollis* and *S. labiatus* in mixed-species troops.

Species	**Quantity**	**150 cm**	**50 cm**	**Z value**
S. fuscicollis	5 items	50.5	47.5	$z = -0.34$, $p > 0.05$
S. fuscicollis	20 items	45.5	59.5	$z = -0.94$, $p > 0.05$
S. labiatus	5 items	27.5	78.0	$z = -2.31$, $\mathbf{p < 0.05}$
S. labiatus	20 items	17.5	32.0	$z = -1.73$, $p > 0.05$

P-values refer to Wilcoxon Signed-Ranks test. Bold indicates a significant result.

Using the same data but re-arranging to show species differences, as in single-species troops, there was no species difference in the latency to obtain a food item from the box with five food items at 150 cm from the ground and *S. labiatus* were significantly faster than *S. fuscicollis* to obtain a food item from the box with twenty food items at 150 cm from the ground (Table 8.6). Unlike in single-species troops, there was no significant species difference for the box with five food items and that with twenty food items at 50 cm from the ground.

Table 8.6: Species differences in median latencies (seconds) to obtain a food item from boxes with five and twenty food items at 150 cm and 50 cm from the ground in mixed-species troops.

Height	**Quantity**	***S. fuscicollis***	***S. labiatus***	**Z value**
150 cm	5 items	50.5	27.5	$z = -1.39$, $p > 0.05$
150 cm	20 items	45.5	17.5	$z = -2.72$, $\mathbf{p < 0.05}$
50 cm	5 items	47.5	78.0	$z = -1.03$, $p > 0.05$
50 cm	20 items	59.5	32.0	$z = -1.16$, $p > 0.05$

P-values refer to Mann-Whitney U test. Bold indicates a significant result.

So, in mixed-species troops, as in single-species troops, *S. labiatus* remained the first to exploit the preferred upper box when it contained twenty food items. In contrast, *S. fuscicollis* in mixed-species troops, unlike in single-species troops, were no longer faster than *S. labiatus* to the lower box with five or twenty food items. If we now compare the behaviour of each species, separately, in single- and mixed-species troops (between conditions) it is found that, *S. fuscicollis* exhibit no difference in their latency to any box in single-species troops compared with mixed-species troops (Table 8.7). So *S. fuscicollis* appear to be unaffected (in their latency to obtain their first food item) by the presence of a *S. labiatus*. *S. labiatus*, however, were faster to obtain a food item from the box with five food items at 150 cm from the ground, and the box with twenty food items at 50 cm from the ground, in mixed-species troops compared with single-species troops. Thus they appear to be facilitated to these boxes when in the presence of a *S. fuscicollis* pair.

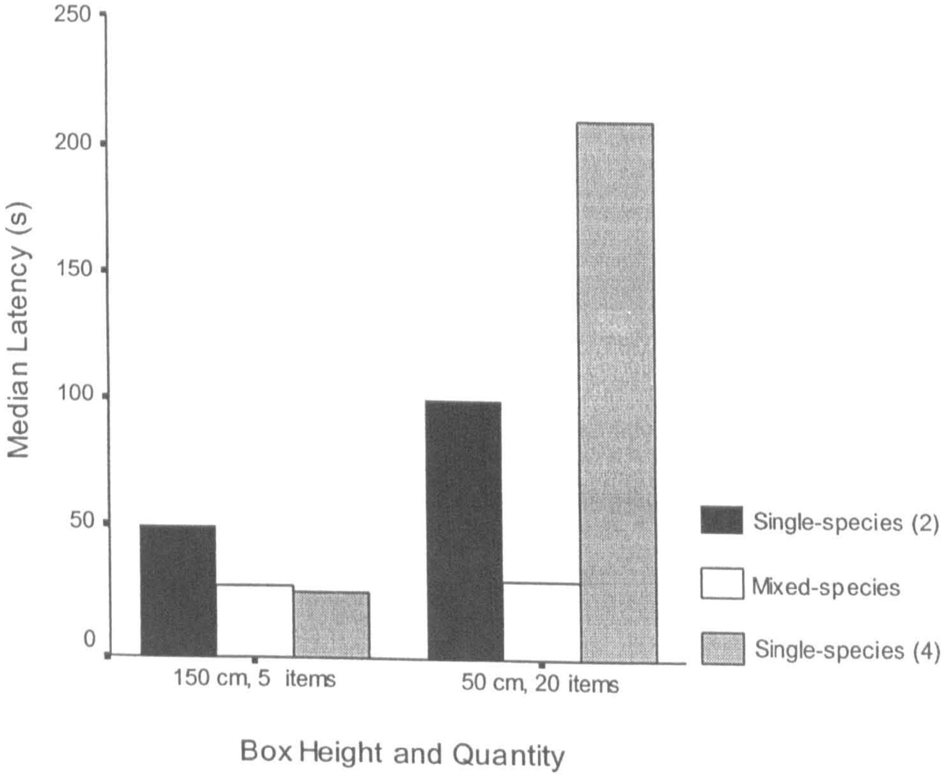
Table 8.7: Median latencies to (seconds) obtain food item from boxes with five and twenty food items at 150 cm and 50 cm for *S. fuscicollis* and *S. labiatus* in single- and in mixed-species troops.

Species	**Height**	**Quantity**	**Single-species troops**	**Mixed-species troops**	**Z value**
S. fuscicollis	150 cm	5 items	30.5	50.5	$z = -0.28$, $p > 0.05$
S. fuscicollis	150 cm	20 items	38.5	45.5	$z = -0.31$, $p > 0.05$
S. fuscicollis	50 cm	5 items	66.0	47.5	$z = -1.41$, $p > 0.05$
S. fuscicollis	50 cm	20 items	65.5	59.5	$z = -0.63$, $p > 0.05$
S. labiatus	150 cm	5 items	49.5	27.5	$z = -2.34$, $\mathbf{p < 0.05}$
S. labiatus	150 cm	20 items	23.5	17.5	$z = -0.98$, $p > 0.05$
S. labiatus	50 cm	5 items	93.5	78.0	$z = -1.60$, $p > 0.05$
S. labiatus	50 cm	20 items	100	32.0	$z = -2.94$, $\mathbf{p < 0.05}$

P-values refer to Wilcoxon Signed-Ranks test. Bold indicates a significant result.

However, this facilitation of *S. labiatus* in mixed-species troops may simply be a result of an increase in troop size, rather than due to the propensities of the *S. fuscicollis* per se. It may be that *S. labiatus* would be similarly facilitated by the presence of another *S. labiatus* pair. To test for this possibility, the results for the six mixed-species troops were compared with those from a single-species troop consisting of four *S. labiatus* (SL1). No statistics were done due to the sample size. We can see from Figure 8.1 that, for the box with five items at 150 cm, *S. labiatus* are facilitated by the presence of a congeneric pair but are similarly facilitated by the presence of a conspecific pair. So the observed facilitation does appear to be simply a consequence of an increase in troop size from two to four individuals. We can see also from Figure 8.1 that, for the box with twenty items at 50 cm from the ground, *S. labiatus* are facilitated by the presence of *S. fuscicollis*, but not by the presence of two additional *S. labiatus*. (In fact, in a single-species troop of four *S. labiatus*, one or more individuals may be excluded from either box by their troop members, resulting in the high median latencies for this condition). So, in this case, we can conclude that the facilitation observed really is a result of association with *S. fuscicollis* per se and not simply due to an increase in troop size.

Figure 8.1: Median latencies (seconds) to obtain food item from the box with five food items at 150 cm from the ground and twenty food items at 50 cm from the ground for *S. labiatus* in single-species troops of two and four individuals and in mixed-species troops.



In mixed-species troops, competitive interactions were observed between the species at all boxes. These generally consisted of attempts by *S. labiatus* to monopolise the food as evidenced by the greater frequency of competitive interactions directed from *S. labiatus* to *S. fuscicollis* (Table 8.8). There was no simple increase in the frequency of competitive interactions with increasing food quantity. However, there were a greater number of competitive interactions at the preferred height (150 cm) than at the non-preferred height (50 cm).

Table 8.8: Direction and total frequency of competitive interactions at each box.

Height	**Quantity**	***S. labiatus* to *S. fuscicollis***	***S. fuscicollis* to *S. labiatus***	**Total**
150 cm	5 items	15	9	**24**
150 cm	20 items	23	7	**30**
50 cm	5 items	15	6	**21**
50 cm	20 items	10	12	**22**
Total		**63**	**34**	**97**

8.4 Discussion

In investigations of general height use in mixed-species troops in captivity, *S. fuscicollis* and *S. labiatus* have been found to segregate themselves vertically with *S. fuscicollis* occupying a lower mean height than their congeners, as is also the case in the wild. This pattern was not evident in this study. Although both species were found to exhibit foraging height preferences in single-species troops, the preference of both species was to forage at a position high in their enclosure (i.e., they were both generally faster to feed from the upper box than the lower box). This pattern is likely to be due to a general reluctance to descend near to the ground, probably due to the perceived threat of terrestrial attack. Although predation is not a real threat in their risk-limited captive environment, both species remain extremely vigilant with regards to terrestrial predators such as feral cats (of which there are many at the zoo) (Prescott, pers. obs). (Thus the important factor in captivity is height relative to ground level). However, although both species preferred the upper box, *S. fuscicollis* were faster than *S. labiatus* to descend to the lower box and obtain a food item from it. This pattern is consistent with data on height preferences in the wild with *S. labiatus* occupying a higher stratum than their congener and rarely descending to the forest floor, whereas *S. fuscicollis* use all levels down to the forest floor (a consequence of them searching tree trunks for embedded, hidden prey) (Yoneda, 1981, 1984a; Pook & Pook, 1982; Hardie, 1998; Buchanan-Smith, 1999). *S. fuscicollis* are thus far more likely to descend to the floor, and often do so in the wild to retrieve insects flushed from higher levels by their congeners (Yoneda, 1981; Terborgh, 1983; Norconk, 1990b; Peres, 1991; Garber, 1992, 1993a). The willingness of *S. fuscicollis* to descend to the lower box observed in this experiment appeared to facilitate *S. labiatus* to do the same in mixed-species troops. (The facilitation was not simply a consequence of an increase in troop size since *S. labiatus* were not similarly facilitated to lower levels by the presence of a conspecific pair). A similar finding was made by Hardie (1995) who found that *S. labiatus* were facilitated in the presence of *S. fuscicollis* to approach and investigate novel non-threatening and threatening objects placed low in an experimental enclosure. *S. labiatus* may be exploiting the vigilance behaviour of *S. fuscicollis* low in the enclosure and are therefore more willing to exploit the lower foraging box in their presence. As such, this is a possible advantage of mixed-species troop formation to *S. labiatus*.

Although the most important predators of tamarins are medium to large-sized diurnal raptors, carnivorous terrestrial mammals, such as small to medium-sized felids and mustelids, are likely to pose a threat to callitrichines (e.g., Buchanan-Smith, 1990a; Heymann, 1990b). These predators hunt by surprise and rely upon stealthy approaches and ambushes. The vigilance behaviour of *S. fuscicollis* is likely to be more effective in detection of such threats since they are more vigilant at lower levels of the forest; they perform more downward scanning and detect more terrestrial and scansorial threats than their congeners (Peres, 1993a, for *S. fuscicollis* and *S. mystax*). By utilising the vigilance behaviour of *S. fuscicollis* in lower strata, and given their dominance over *S. fuscicollis*, *S. labiatus* may be more able to investigate and utilise potentially beneficial objects occurring in this area in the presence of *S. fuscicollis*. Support for the idea that the congeners of *S. fuscicollis* utilise their vigilance behaviour of lower strata comes from observations in the wild. For example, during a trapping program, *S. labiatus* descended to traps placed at a height of about 1 metre from ground level only after the associated troop of *S. fuscicollis* had been eating the bait for 2 - 3 days. At no time did *S. labiatus* approach the traps unless *S. fuscicollis* were present (Buchanan-Smith, 1989). Similarly, *S. mystax* appear to be extremely cautious of descending to the forest floor, and have only been seen to do so when in association with *S. fuscicollis* (Heymann, pers. obs.). Returning to this experiment, it is a little puzzling that, given that *S. labiatus* were facilitated to the box with twenty food items at 50 cm from the ground, they were not similarly facilitated to the box with five food items at 50 cm from the ground. Perhaps, they did not wish to descend to what they probably perceived as a dangerous location when the food reward was only a small one.

S. labiatus were also facilitated to the box with five food items at 150 cm from the ground in the presence of a congeneric pair. However, since they were facilitated to this box by a conspecific pair also, this facilitatory effect was probably due to an increase in troop size rather than due to the propensities of *S. fuscicollis* per se. Perhaps *S. labiatus* were quicker to this box in conditions with four individuals because they perceived themselves to be in competition with more individuals for the food. However, if this were the case, one would have expected to see facilitation for the box with twenty food items at 150 cm from the ground also. Given that no such facilitation occurred, this explanation must remain a tentative one.

In mixed-species troops, *S. labiatus* were faster than *S. fuscicollis* to obtain a food item from the box with five food items at the preferred height of 150 cm from the ground.

The *S. labiatus*, in fact, reached the box first and proceeded to try to exclude *S. fuscicollis* from the food using threats, agonistic behaviour and displacements, often with success. In fact, competitive interactions took place at all boxes, the majority of which were directed from *S. labiatus* to *S. fuscicollis*. This is consistent with field reports of competitive exclusion of *S. fuscicollis* by dominant *S. labiatus* in the wild (Yoneda, 1981; Pook & Pook, 1982; Buchanan-Smith, 1989, 1990a) and constitutes a disadvantage of mixed-species troops formation to *S. fuscicollis*. The degree of inter-specific feeding competition for plant resources shown in wild mixed-species troops of *S. fuscicollis* and *S. mystax* has been shown to be a function of the size of resources 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-feeding trees, which can be monopolised by one species, there may be conflict between individuals in the mixed-species troop. 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 *S. fuscicollis* from consuming food until they themselves are satiated (Terborgh, 1983; Buchanan-Smith, 1990a; Heymann, 1990a; Norconk, 1990b; Peres, 1996). In this experiment, there was no increase in the frequency of competitive interactions with increasing food quantity. It is likely that both five and twenty mealworms, contained as they were in a foraging box and concealed beneath wood shavings, were perceived as a small, monopoliseable resource by the tamarins. However, there were a greater number of competitive interactions at the preferred height (150 cm) than at the non-preferred height (50 cm). Both species may have felt more secure higher up in the enclosure and were thus more willing to defend the food there.

The finding that, in mixed-species troops, *S. labiatus* attempt to prevent *S. fuscicollis* from obtaining food from the box at the preferred height led me to investigate what would happen if two boxes were presented simultaneously, each with a different quantity of food, and the greater quantity presented at the non-preferred height? In this instance, would *S. labiatus* in mixed-species troops take advantage of their dominant status and, trading-off preferred height against quantity, take precedence and descend to the less-preferred height to monopolise the food there? This question was investigated in Experiment 5.

8.5 Experiment 5: Foraging Height Preferences and Feeding Competition (Two Boxes Present Simultaneously).

The aim of the experiment was to investigate whether foraging height preferences alter when the monkeys are given a choice between two quantities of food presented simultaneously at different heights; and hence whether the monkeys would trade-off food quantity against preferred foraging height.

8.5.1 Study Animals

The study animals were those tested in Experiment 4 (see Section 8.2.1) but with the exclusion of SF1 and SL1. Troops were tested as both single-species troops and mixed-species troops (SF3 & SL2, SF4 & SL4, SF5 & SL5, SF6 & SL6, SF9 & SL7, SF11 & SL11).

8.5.2 Design

The experimental design was as in Experiment 4 (see Section 8.2.2) except that two boxes were presented in each test trial as opposed to one. Each troop received two test trials as a single-species troop and two as a mixed-species troop; one in which five mealworms were presented at 50 cm and twenty at 150 cm from the ground, and one in which twenty mealworms were presented at 50 cm and five at 150 cm from the ground. Again, the order of trial presentation was counterbalanced across troops, and half the troops were tested as single-species troops first and mixed-species troops second and the other half the reverse, to control for order effects. The experiment began the day after Experiment 4 and was conducted between June and September, 1996, and between June and August, 1997.

8.5.3 Procedure

The experiment consisted of test trials only (i.e., no pre-training or training trials were necessary). The procedure for these trials was as in Experiment 4 (see Section 8.2.3) except that, as described above, two foraging boxes were presented simultaneously in each test trial, one at 50 cm and one at 150 cm from the ground, each containing a different quantity of food (five or twenty mealworms).

8.5.4 Recording Methods

Recording methods were exactly as in Experiment 4 (see Section 8.2.4).

8.5.5 Data Analysis

Data analysis was exactly as in Experiment 4 (see Section 8.2.5). Again, there was little difference in the pattern of latencies to approach within 15 cm of the box, touch the box, and obtain the first food item. Consequently, only data for the latency for each monkey to obtain their first food item will be presented. In addition, data on the direction and total frequency of competitive interactions are also presented.

8.6 Results

Single-species Troops

Considering the single-species troop data first, in single-species troops of two individuals, *S. fuscicollis* were significantly faster to obtain a food item from the box with twenty food items at 150 cm from the ground than from that with five food items at 50 cm from the ground (Table 8.9). There was no significant difference in their latency to obtain a food item from the box with twenty food items at 50 cm from the ground and that with five food items at 150 cm from the ground. *S. labiatus* were significantly faster to obtain a food item from the box with twenty food items than from that with five food items, regardless of whether it was presented at 150 cm or 50 cm from the ground.

Table 8.9: Median latencies (seconds) to obtain a food item from boxes presented simultaneously with five and twenty food items at 150 cm and 50 cm from the ground for *S. fuscicollis* and *S. labiatus* in single-species troops.

Species	**Height and Quantity**	**Latency**	**Z value**
S. fuscicollis	150 cm, 20 items	16.0	
S. fuscicollis	50 cm, 5 items	127.5	$z = -3.06$, $\mathbf{p < 0.05}$
S. fuscicollis	50 cm, 20 items	45.5	
S. fuscicollis	150 cm, 5 items	94.0	$z = -1.77$, $p > 0.05$
S. labiatus	150 cm, 20 items	14.0	
S. labiatus	50 cm, 5 items	115.0	$z = -3.06$, $\mathbf{p < 0.05}$
S. labiatus	50 cm, 20 items	46.5	
S. labiatus	150 cm, 5 items	111.0	$z = -2.51$, $\mathbf{p < 0.05}$

P-values refer to Wilcoxon Signed-Ranks test. Bold indicates a significant result.

So, as one would expect, both species are faster to the box containing the greater quantity of food when it is presented at the preferred height. When the greater quantity is presented at the non-preferred height, *S. labiatus* appear to trade-off preferred height for the greater quantity of food.

Mixed-species Troops

How are these preferences altered in mixed-species troops? In mixed-species troops, as in single-species troops, *S. labiatus* were significantly faster to obtain a food item from the box with twenty food items at 150 cm from the ground than from that with five food items at 50 cm from the ground (Table 8.10). In fact, they often did not obtain any food from the box with five items at all as evidenced by the ceiling value (1200 seconds) for this box. In contrast to *S. labiatus*, in mixed-species troops *S. fuscicollis* showed the reverse of the pattern they exhibited in single-species troops, and were significantly faster to obtain a food item from the box with five food items at 50 cm from the ground than from that with twenty food items at 150 cm from the ground. They often did not obtain any food from the box with twenty items at all as evidenced by the ceiling value for this box. Neither species showed a significant difference in their latency to obtain a food item from the boxes with five and twenty food items at 150 cm and 50 cm from the ground respectively.

Table 8.10: Median latencies (seconds) to obtain food item from boxes presented simultaneously with five and twenty food items at 150 cm and 50 cm for *S. fuscicollis* and *S. labiatus* in mixed-species troops.

Species	**Height and Quantity**	**Latency**	**Z value**
S. fuscicollis	150 cm, 20 items	1200.0	
S. fuscicollis	50 cm, 5 items	25.5	$z = -2.67$, **$p < 0.05$**
S. labiatus	150 cm, 20 items	16.5	
S. labiatus	50 cm, 5 items	1200.0	$z = -3.06$, **$p < 0.05$**
S. fuscicollis	50 cm, 20 items	28.5	
S. fuscicollis	150 cm, 5 items	23.5	$z = -0.43$, $p > 0.05$
S. labiatus	50 cm, 20 items	1200.0	
S. labiatus	150 cm, 5 items	1200.0	$z = -1.78$, $p > 0.05$

P-values refer to Wilcoxon Signed-Ranks test. Bold indicates a significant result.

Using the same data but re-arranging to show species differences, *S. labiatus* were significantly faster than *S. fuscicollis* to obtain a food item from the box with twenty items at 150 cm from the ground, whilst *S. fuscicollis* were significantly faster than *S. labiatus* to obtain a food item from the box with five food items at 50 cm from the ground (Table 8.11). There was no species difference in the latency to obtain a food item from the box with twenty food items at 50 cm from the ground, but *S. fuscicollis* were significantly faster than *S. labiatus* to obtain a food item from the box with five food items at 150 cm from the ground.

Table 8.11: Species differences in median latencies (seconds) to obtain a food item from boxes presented simultaneously with five and twenty food items at 150 cm and 50 cm from the ground in mixed-species troops.

Height and Quantity	***S. fuscicollis***	***S. labiatus***	**Z value**
150 cm, 20 items	1200.0	16.5	z = - 3.65, **$p < 0.05$**
50 cm, 5 items	25.5	1200.0	z = - 4.45, **$p < 0.05$**
50 cm, 20 items	28.5	1200.0	z = - 1.96, $p > 0.05$
150 cm, 5 items	23.5	1200.0	z = - 4.31, **$p < 0.05$**

P-values refer to Mann-Whitney U-test. Bold indicates a significant result.

So, when the greater quantity of food was presented at the preferred height, in mixed-species troops, *S. labiatus* went straight to this box and monopolised the food there. This is illustrated by the relatively high frequency of competitive interactions directed from *S. labiatus* to *S. fuscicollis* at this box (Table 8.12). In contrast, *S. fuscicollis*, which also preferred this box in single-species troops, in mixed-species troops instead proceeded to utilise the box with the lesser quantity of food at the non-preferred height and ate all the food there. This was probably due to *S. labiatus* reaching the rich box first and monopolising it. This pattern is reflected in Table 8.13 which compares the behaviour of each species in single- and in mixed-species troops. *S. labiatus* exhibit no difference in their latency to the box with twenty items at 150 cm from the ground in single-species and mixed-species troops, whilst *S. fuscicollis*, in contrast, were faster to the box with five items at 50 cm from the ground in mixed-species troops than in single-species troops. As a consequence of the species utilising different boxes when in mixed-species troops, *S. labiatus* were slower to the box with five items at 50 cm from the ground and *S. fuscicollis* slower to the box with twenty items at 150 cm from the ground in mixed-species troops than in single-species troops.

Table 8.12: Direction and total frequency of competitive interactions at each box.

Height and Quantity	***S. labiatus* to *S. fuscicollis***	***S. fuscicollis* to *S. labiatus***	**Total**
150 cm, 20 items	15	6	**21**
50 cm, 5 items	0	0	**0**
50 cm, 20 items	8	4	**12**
150 cm, 5 items	2	0	**2**
Total	**25**	**10**	**35**

Table 8.13: Median latencies to (seconds) obtain food item from boxes presented simultaneously with five and twenty food items at 150 cm and 50 cm for *S. fuscicollis* and *S. labiatus* in single- and in mixed-species troops.

Species	**Height and Quantity**	**Single-species troops**	**Mixed-species troops**	**Z value**
S. fuscicollis	150 cm, 20 items	16.0	1200.0	z = - 2.98, **p < 0.05**
S. fuscicollis	50 cm, 5 items	127.5	25.5	z = - 2.98, **p < 0.05**
S. labiatus	150 cm, 20 items	14.0	16.5	z = - 1.43, p > 0.05
S. labiatus	50 cm, 5 items	115.0	1200.0	z = - 3.06, **p < 0.05**
S. fuscicollis	50 cm, 20 items	45.5	28.5	z = - 1.80, p > 0.05
S. fuscicollis	150 cm, 5 items	94.0	23.5	z = - 2.35, **p < 0.05**
S. labiatus	50 cm, 20 items	46.5	1200.0	z = - 2.28, **p < 0.05**
S. labiatus	150 cm, 5 items	111.0	1200.0	z = - 2.98, p > 0.05

P-values refer to Wilcoxon Signed-Ranks test. Bold indicates a significant result.

When the greater quantity of food is presented at the non-preferred height the results are a little more complex. *S. fuscicollis* were as fast to this box as they were in single-species troops but were faster to the box with the lesser quantity of food also (Table 8.13). This is probably because they were again displaced from the box with the greater quantity of food by *S. labiatus* (Table 8.12). However, *S. labiatus* in mixed-species troops showed great variation in their latency to obtain a food item from the box with the greater quantity of food at the non-preferred height. They were slower to this box in mixed-species troops than in single-species troops but were no slower than *S. fuscicollis* in mixed-species troops (Table 8.11). This is an indication of their displacement of *S. fuscicollis* at this box. *S. labiatus* were as slow to the box with the lesser quantity of food at the preferred height in mixed-species troops as they in single-species troops and generally did not obtain any food from this box.

8.7 Discussion

If two foraging boxes are presented simultaneously at 150 cm and 50 cm from the ground, and the tamarins have received training to recognise that different designs on the boxes indicate that they contain one of two possible quantities of food, in single-species troops, *S. fuscicollis* prefer to feed from the box containing the greater quantity of food items (i.e., the latency to the box with greater quantity of food items is less than that with the lesser quantity of food items) when it is presented at the preferred height. *S. labiatus* in single-species troops prefer this box regardless of the height at which it is presented. So *S. labiatus*, at least, will trade-off their preferred foraging height for food quantity. This would appear to provide confirmation that they had learnt the significance of the designs on the boxes. It has been suggested that wild tamarins may use local visual cues closely associated with the presence of insect prey (e.g., damaged foliage, rolled leaves) to increase their likelihood of encounter with these food types (Terborgh, 1983). Perhaps the apparent ability of *S. labiatus* to learn to associate a particular patterned design with food quantity is a reflection of this. The fact that the majority of competitive interactions occurred at the box with the greater quantity of food items may also be an indication that *S. labiatus* had learnt the significance of the designs. (A clearer test of the ability to learn the significance of the cues would have been to have present two boxes with different quantities of food simultaneously but at the same height).

In mixed-species troops, when the box with the greater quantity of food is presented at the preferred height, *S. labiatus* being dominant to *S. fuscicollis*, were able to maintain their preference for this box and aggressively monopolised the food there, preventing *S. fuscicollis* from obtaining any food from this box. *S. fuscicollis*, excluded from this box, instead utilised the box with the lesser quantity of food at the non-preferred height. When the box with the greater quantity of food is presented at the non-preferred height, some *S. fuscicollis* proceeded to utilise it but were displaced from it by *S. labiatus* and then proceeded to utilise the box with the lesser quantity of food. Thus, one cost incurred to *S. fuscicollis* in mixed-species troops in captivity is having to alter/confine its foraging to sub-optimal heights. So, to some extent vertical segregation during foraging in mixed-species troops in captivity is a consequence of competitive displacement. Thus, although vertical segregation during foraging between associating species in the wild is almost certainly a consequence of the behavioural and morphological adaptation to the separate strata in which their particular insect prey are found, it may also be a consequence of competitive displacement; *S. fuscicollis* being forced to forage at lower heights in the presence of their dominant congeners. Whatever the case, vertical segregation plays an important role in niche separation for these species in mixed-species troops.

8.8 Conclusion

Foraging height preferences were investigated in captive *S. fuscicollis* and *S. labiatus*. Both species were found to prefer to forage at a position high in their enclosure than near to the ground. However, *S. fuscicollis* were found to be more willing than *S. labiatus* to descend to low in the enclosure which is consistent with their height use in the wild. The willingness of *S. fuscicollis* to descend to near the ground facilitated *S. labiatus* to do the same in mixed-species troops and this facilitation was not likely to be due to a simple increase in troop size. *S. labiatus* may be using the vigilance behaviour of *S. fuscicollis* low in the enclosure and as such this is a possible advantage of mixed-species troops formation to *S. labiatus*.

Foraging height preferences were also altered for *S. fuscicollis* in the presence of *S. labiatus*. When two foraging boxes were presented simultaneously at different heights, each with a different quantity of food, *S. labiatus* were found to monopolise the box with greater quantity of food and displace *S. fuscicollis* to the poorer box (especially when this box was at the non-preferred height). This provides evidence that *S. labiatus* can learn to associate a particular patterned design on the foraging box with food quantity which may be a refection of their use of cues during foraging for insect prey. Thus, in the wild, although vertical segregation corresponds to the searching of specific microhabitats for insect prey, it may also be, to some extent, a consequence of competitive displacement.

The competitive displacement of *S. fuscicollis* by *S. labiatus* in captivity is consistent with reports of competitive exclusion of *S. fuscicollis* by their dominant congeners in the wild and constitutes a disadvantage to *S. fuscicollis* in mixed-species troops. In the captive experiments, when a single foraging box was presented to the monkeys, competitive interactions were less frequent than when two boxes were presented simultaneously. Obviously, with two food sources both species were able to obtain food by separating (although *S. labiatus* were able to monopolise the richer box). This has implications for the captive care of tamarin mixed-species troops.

Chapter 9

Social Learning About Food Location

"Frugivorous forest primates face a continual challenge to locate ripe fruit due to the poor visibility characterising a heavily vegetated habitat and the spatial and temporal unpredictability of their fruit resources."

[Olupot et al., *1998: p. 339]*

9.1 Introduction

Local enhancement (Thorpe, 1963) is the term often used to describe the process by which an individual's attention is directed to the location of food by the foraging or feeding behaviour of other individuals. Throughout the 1960s and early 1970s, several authors argued that local enhancement might give birds foraging in a flock a significant foraging advantage over solitary birds if they can capitalise upon the food finds of their flock-mates (Crook, 1965; Newton, 1967; Lack, 1968; Zahavi, 1971; Ward & Zahavi, 1973). Such an advantage applies particularly to birds whose food occurs in localised patches and is abundant within those patches, for example graminivores and frugivores. It was suggested that, provided the patches contain enough food for all, then mean rate of food intake for flocking birds will be increased (compared to that of solitary birds).

With the advent of optimal foraging theory, such arguments became more formalised and it was suggested that, in addition to increasing mean rate of food intake, social foraging can reduce variation in food intake also (Thompson *et al.*, 1974; Pulliam & Millikan, 1982). For example, in computer simulations, Thompson *et al.* (1974) found that flocking and solitary birds had about the same mean feeding rates but that individuals in flocks experienced less risk of starvation because they were less likely to go for long periods of time without finding food. They found, also, that the benefit of flocking was greater when food was more patchily distributed. Their concluding statement was that "*minimising risk is an important consequence of flocking*" and that it may be more important than maximising feeding rate. The model of Thompson *et al.* was based upon specific assumptions about prey detectability and bird movement patterns. Pulliam and Millikan (1982) developed a more simple and more general model, free of these restrictions, and inspired by Schaffer's (1978) model of reciprocation and by the work of Caraco (1980, 1981a,b) and Caraco *et al.* (1980a) on risk aversion. Social foraging was found to be advantageous only when a single forager cannot eat all of the food in a patch before the food would otherwise disappear (i.e., if the patches disappear in much less time than would otherwise be required for the food to be completely consumed, then the presence of additional group members hardly affects per capita consumption). Such a rule applies to animals feeding on temporally patchy resources, such as insectivorous birds (e.g., swallows) and primates (e.g., chimpanzees, tamarins) feeding on ephemeral swarms of insects, and frugivorous birds (e.g., parrots, tanagers, turacos) and primates (e.g., tamarins) feeding on ripe fruit that may soon rot or fall to the ground. So the advantage of social foraging increases as food resources become more patchily distributed, not only in space, but also in time.

The models described above consider group foragers relative to solitary foragers. However, the advantages of foraging in a social group that arise through local enhancement can be expected to increase with increasing group size. Also as a direct consequence of individuals sharing information about discoveries of concealed food, increasing group size can increase the rate at which patches of food are discovered in spatially and temporally uncertain environments. This may result in an increase in individual mean rate of food intake and a decrease in the variance in this intake for group members. Since an increase in troop size is a consequence of mixed-species troop formation, one might expect individual tamarins in mixed-species troops to increase their foraging efficiency in this way, especially given the spatial and temporal distribution of their major food resources: ripe fruit and insects. The fruit species taken by tamarins are characterised by a scattered and patchy spatial distribution and the production of small amounts of ripe fruit each day (Janson *et al.*, 1981; Terborgh, 1983, 1985; Yoneda, 1984b; Crandlemire-Sacco, 1986; Garber, 1986, 1988a,b; Soini, 1987). Although, individual fruiting trees or patches of fruiting trees are often exploited in a co-ordinated manner, with trees of the same species being visited during successive feeding bouts, these may be separated by some 90 - 140 metres (Garber, 1993a; Garber & Hannon, 1993). Relative to fruit, insects are more diffuse in the environment. However, their spatial distribution is linked to their particular plant prey or reproductive host species. Remembering the locations of multiple, scattered fruit and insect patches, separated by distances far outside the field of view, is likely to place considerable demands upon the spatial mapping abilities of tamarins. Being alerted to the location of these by other troop members may thus be advantageous over and above individual spatial knowledge.

With regards the temporal distribution of food resources, insect communities in the rain forest may undergo marked diurnal and seasonal changes in abundance, diversity and taxonomic composition (Janzen, 1973; Smythe, 1974; Ricklef, 1975; Terborgh, 1983). Such variation in the temporal distribution of insect prey is likely to have a major impact on tamarin foraging decisions and foraging success (Garber, 1993b). With regards fruit resources, some species taken by tamarins fruit asynchronously within species (e.g., *Ficus* spp.) and some between species (e.g., *Inga* spp.) (e.g., Peres, 1993b, 1996). This makes it very difficult to predict when a particular tree, patch of trees, or species is about to fruit. Individual tamarins would obviously benefit if they could be alerted to the location of ripe fruit in these by other troop members (local enhancement). The majority of tamarin fruit species, though, exhibit a high degree of intra-specific fruiting synchrony (Garber, 1993a). However, although fruiting time is predictable for these species, it may remain difficult to identify exactly which particular trees or patches of trees within the home range are about to fruit (due, for example, to variations in local age distribution or edaphic conditions). So, even for synchronously ripening fruit species, foraging tamarins can benefit from the patch finds of their troop-mates, and once feeding within a patch, profit from their finds of ripe fruit.

Having said this, however, since associating tamarin species move about their whole range as a cohesive unit, and given that poor visibility characterises their densely vegetated habitat, it is less likely that they benefit through local enhancement in this way compared to, say, flocking birds able to visually scan large areas for food or feeding aggregations as they fly over them (e.g., vultures, geese), or to central-place foragers (e.g., herons, corvids, bats). However, the operation of local enhancement will be clearly advantageous in mixed-species groups, if participating species possess an inequality of or divergent knowledge concerning food resources. This is conceivable for species whose ranging does not wholly coincide in time and space. In such situations, the foraging efficiency of individuals of one species will obviously be increased if they can join with the other species and capitalise upon the food finds of individuals of that species as well as those of their own. As long as food is on the whole clumped, and contains more than enough for individuals of both species, mixed-species groups may be mutually profitable. As described in Chapter 7, given the vertical stratification between associating tamarin species, mixed-species tamarin troops may accrue a foraging advantage in this way in as much as food patches which are potentially quite accessible occur at heights not normally inspected by both species in the mixed-species troops. Combining the search effort of the different species in the separate strata may thus increase the total searching range of the whole troop. In this regard, Peres (1996) has documented that *S. mystax* are more often the first to encounter large, productive food patches located high in the forest, at heights not normally traversed by their congeners, whereas *S. fuscicollis* are more often first to smaller, less productive food patches lower in the forest.

While these findings suggest some inequality of knowledge, it is still possible that both species know about the location of the patches in the separate strata. This reflects the difficulty in gathering evidence for local enhancement acting to increase foraging efficiency in social foragers in the field because one cannot control for previous experience. Experimental studies of foraging, however, allow one to control both previous experience and the amount of information available to the forager. Experimental evidence for an increase in flock size increasing foraging efficiency through local enhancement has been provided by Krebs *et al.* (1972) who placed *Parus major* (great tit) in experimental aviaries containing artificial trees made of dowels. Observations revealed that the fraction of birds finding food in a 15 minute period increased with increasing flock size (25 %: single bird; 40 %: pair; 75 %: four birds), and that this increase was due to fine scale local enhancement. After one individual in the flock had located food, the other members of the flock would immediately abandon their searching and fly to the perch upon which the food was situated. Moreover, by varying the amount of food found in each of the containers, Krebs *et al.* showed that local enhancement was stronger when food was more concentrated within patches. The local enhancement demonstrated by Krebs *et al.* resulted from more birds searching for a limited amount of food. Given enough time, the birds in a flock of any size would have found all of the food available, meaning that larger flocks could not have resulted in a greater mean rate of food intake. Nevertheless, what the experiments of Krebs *et al.* do clearly demonstrate, is that local enhancement can reduce the variance in an individual's feeding rate.

Krebs (1973) recognised that the advantages of social foraging need not be confined to single-species groups, provided that associating species eat similar types of food, or at least food that occurs in similar places. In an experiment with mixed-species flocks of *P. atricapillus* (black-capped chickadee) and *P. rufescens* (chestnut-backed chickadee) he found that, following the finding of a single food item by a flock member of either species, both species modified their searching behaviour, increasing their search effort in the location where the food was found even when the two species had been trained to forage in different niches. That is, the two species converged in their foraging behaviour as a result of local enhancement. Furthermore, Krebs demonstrated that this social learning enhanced the learning of novel feeding sites in that naïve individuals learned to look in/utilise a particular type of feeding site (a foil basket) when in the presence of a congener who was experienced regarding the novel feeding site.

In contrast to the findings of Krebs, Morse (1970) found that mixed flocks of insectivorous birds tended to diverge (become more specialised) in their foraging behaviour in the presence of ecologically similar species (i.e., niche overlap became smaller when the birds were in mixed species flocks). He suggested that this increased specialisation in the presence of the congener results from interactions on the part of the dominant species, forcing the subordinate species into a more highly specialised niche. Thus, advantages to social foragers through local enhancement may not be accrued by all individuals equally. Baker *et al.* (1981) conducted similar aviary experiments with *Junco hyemalis* (dark-eyed junco). They reported that dominant birds found more seeds when feeding in flocks than when feeding alone. Subordinate birds did not, but their variance in food intake was reduced. Baker *et al.* (1981) concluded that subordinates join flocks in order to reduce their chances of finding insufficient food.

Given this background, I designed an experiment (Experiment 6) to investigate whether tamarins in mixed-species troops benefit, through local enhancement, by paying attention to the food finds of their troop-mates (i.e., by learning from others about the location of food on quite a fine scale). Moreover, by the use of different food cache locations, I was able to investigate what level of their fine scale environment the tamarins respond to after a food find (i.e., what they cue in upon, e.g., the same tree, same branch height or same branch) and hence whether they learn from their troop-mates about not just the location of a food cache but also the type of location in which food caches are to be found. As described in Chapter 2, if individuals are able to share or parasitise the knowledge of other troop members, then foraging in mixed-species troops may be more efficient than in single-species troops in that sources of information may be better or more numerous owing to the increased number of individuals in a mixed-species troop. I was also interested in whether participating species benefit equally (given the dominance of *S. labiatus* over *S. fuscicollis*), and whether any benefit varies with distribution of food in the environment. That is, if food occurs in a location habitually searched by one species but not the other, how does this affect local enhancement? (Experiment 7).

9.2 Experiment 6: Local Enhancement When Foraging in the Same Niche

The aims of the experiment were to determine if individual S. fuscicollis *and* S. labiatus *modify their searching behaviour after a conspecific or congener finds a food cache; and to identify what level of their fine scale environment the monkeys respond to following such a find.*

9.2.1 Study Animals

The study animals were six troops of *S. fuscicollis* (SF1, SF3, SF4, SF5: Table 4.1; SF6, SF11: Table 4.3) and six troops of *S. labiatus* (SL1, SL2, SL4, SL5: Table 4.2; SL6, SL11: Table 4.4) housed in separate indoor/outdoor enclosures in the 'Old-Marmoset House'. Further details of housing and husbandry are given in Chapter 4 (Section 4.6). Normally maintained as mixed-species troops, the monkeys were tested as either single-species troops (SF1, SL1), or as both single-species troops and mixed-species troops (SF3 & SL11, SF4 & SL4, SF5 & SL5, SF6 & SL6, SF11 & SL2). All troops consisted of an adult male-female pair together with any offspring, of which only the adult pair were tested. SF1 and SL1 were an exception to this. Both consisted of an adult male-female pair and their sub-adult son and daughter, all of which were tested. Comparing the data from SF1 and SL1 with that of the mixed-species troops acted as a control for troop size effects.

9.2.2 The Foraging Task

Mixed-species troops were required to search for a small cache of food hidden at one of three heights in one of two experimental trees. The 'End-Enclosure' was arranged as an experimental testing area, that is, the network of branches in the enclosure was manipulated to create two discrete but connected food trees, one at either end of the enclosure. Each tree had a cluster of branches, radiating from its trunk, at approximately 100 cm, 150 cm and 200 cm from the ground. Three cylindrical, black, plastic photographic-film cases (5 cm high and 3 cm in diameter, hereafter referred to as 'cases') were attached to two horizontal branches in each cluster (chosen branches were orientated at or near 180° to each other). The cases were 30 cm apart and were present only during training and test trials. Some of the cases were loaded with mealworms (the location of which depended on experimental condition) which were hidden by placing a 2 cm layer of wood shavings on top of them. A 2 cm layer of wood shavings was also placed in all other cases. The fact that all cases contained wood shavings meant that the monkeys could not tell which of the cases contained food simply by scanning from above. Instead, in order to see if a case contained food, it was necessary for the monkeys to approach the case, flick out most of the wood shavings with their hands, and rake through the remainder. This they learned to do readily (Plate 12).

9.2.3 Design

Each troop received six daily test trials as a single-species troop and six as a mixed-species troop (except SF1 and SL1 which were tested as single-species troops only). Six troops received the single-species testing first and mixed-species testing second, and four the reverse, to control for order effects. All mixed-species troops had been mixed prior to experimentation and thus those receiving the single-species testing first required only 2 days habituation to their congeners upon re-mixing for the mixed-species testing. During a test trial, a single case on one of the branches in one of the trees contained five food items. This meant that, due to the concentration of food in a single case, only one individual could obtain the food (unless it was intercepted whilst eating). The location of this case (i.e., branch, tree, branch height) was appropriately counterbalanced between test trials and within and between troops. In the mixed-species trials, it was purely a matter of chance whether *S. fuscicollis* or *S. labiatus* found the food.

By looking for changes in the pattern of searching behaviour of one species after a food find by members of its own species and members of another species it was possible to determine whether intra-specific and inter-specific local enhancement occurs, and whether these occur in both species. In addition, the experimental design allowed me to identify

Plate 12: *S. labiatus* inspecting a case for mealworms after clearing it of wood shavings.

exactly what level of their fine scale environment the monkeys respond to after a food find by another troop member (i.e., what they are cued in upon, if anything, during searching after a food find: the same tree, same branch height, or same branch). The experiment was conducted between May and September, 1996, and between May and July, 1997.

9.2.3 Procedure

Pre-training, training and test trials were conducted before the monkeys' daily feed to ensure they were motivated to search for the food items. Pre-training trials were conducted in the outdoor portions of the monkeys' enclosures (C10 and C11). Training and test trials were conducted in the 'End-Enclosure'. Outwith experimentation, the monkeys were allowed to travel freely between the indoor and outdoor portions of their enclosures and the 'End-Enclosure', except for when the experimenter was setting up the experimental food distributions, at which time they were contained inside the indoor portion of their enclosures. Troops which were not being trained or tested were housed in the indoor portions of their respective enclosures (C1 - C9 and C12 - C18) during training and testing to prevent observation of the experimental task and the location of the food finds of other troops. The experimental procedure was as follows:

(1) *Pre-training Trials*

The monkeys received a basic pre-training, to ensure they were familiar with obtaining food from the cases, during which ten cases were distributed randomly about the branches of the outdoor portion of their enclosure, each containing two food items, at first uncovered, and later covered with wood shavings. Pre-training trials lasted 20 minutes and were given twice daily until all individuals were observed to readily obtain food from the cases by searching through the wood shavings. The cases were present only during the 20 minute trial.

(2) *Training Trials*

During training trials, the monkeys were trained to search in the cases for 'dispersed' food, that is, each case contained a single food item. Each troop received four consecutive daily training trials before the start of testing and one training trial between every subsequent test trial (only one training trial and/or test trial was given per day for each troop). This served to maintain the monkeys' searching effort during the test trials. Training trials lasted until 10 minutes after the last food item was found.

(3) *Test Trials*

Each troop received six consecutive daily test trials (interspersed between training trials), the first of which began immediately after the fourth training trial. The testing procedure consisted of confining the monkeys indoors whilst all cases were cleaned free of debris and a fresh 2 cm layer of wood shavings placed into them. Five food items were then hidden beneath the shavings in the appropriate case. The monkeys were then released into the 'End-Enclosure' (via a wire pulley operated from outside of the enclosure) through the outdoor portion of their enclosure(s) (C10 and C11), and permitted to search for food whilst under observation by the experimenter. Test trials lasted until 10 minutes after the food was found, or if there was no find, for 20 minutes. If a monkey found the food within 1 minute, the test was abandoned as at least 1 minute of data prior to the food find was needed for data analysis. In all, 102 useable tests in which the monkeys found food, but not sooner than 1 minute, were obtained, six for each of the single-species troops and six for each of the mixed-species troops.

9.2.5 Recording Methods

I visually scanned the whole troop, continuously left to right, and dictated into a miniature tape recorder a verbal record of all instances in which an individual visited a particular case (all-occurrences behavioural sampling: Altmann, 1974). Cases were coded to aid recording (e.g., 'Bu1' denoted tree 'B', upper branch, case number 1). Visits were either looks (i.e., the animal peered into the case but did not insert its hands into the case) or searches (i.e., the animal actively manipulated the wood shavings, cupping them or flicking them out of the case, in order to see if a food item was concealed beneath them) but shall hereafter be referred to simply as searches. The time spent searching each case was not recorded. In addition, I recorded the time at which the food cache was found, and by whom, and any food calls and competitive interactions (food stealing, agonistic behaviour and displacements: see Table 4.5) together with the identity of the individuals involved (actor/s and reciever/s). Data from the audio-tapes were transcribed onto record sheets.

9.2.6 Data Analysis

In order to examine the effect of one monkey's finding of the food cache on the searching behaviour of the other troop members, I compared the searching pattern of the monkeys immediately before and after the find. For each species, comparisons were made separately for the food-finder and the non-finders in each troop. The data were divided into 1 minute intervals and the following variables calculated for the minute immediately before and minute immediately after the food find:

(i) [1] percentage of searches on the branch on which the food was found (food branch);

(ii) [1] percentage of searches in the tree in which the food found (food tree), excluding visits to the food branch;

(iii) [1] percentage of searches at the same branch height as the food find (upper, middle, lower), excluding visits to the food tree;

(iv) searching rate (number of cases searched per monkey / minute).

Before and after the food find were compared with the Binomial Test for all troops excluding SF1 and SL1. The Binomial Test is used to examine if, in a series of non-independent observations, there is a change in the underlying theoretical model which is assumed to generate the data (i.e., in this experiment, if the searching behaviour of the tamarins altered after the food find). The test proportion was set at 0.5.

From the data collected, I also calculated the latency (in seconds) from entering the 'End-Enclosure' to finding the food cache, and the number of food calls given by the food finder during the 30 second period after the food find. Comparisons between single-species and mixed-species troops were made for these variables using the Mann-Whitney U test for all troops excluding SF1 and SL1 (although the single- and mixed-species troop data sets were not wholly independent). Significance was set at alpha < 0.05. Competitive interactions were so few as to not warrant statistical analysis.

---

[1] The actual figures on which the percentage values are based are variable, depending upon the number of searches at that locality (i.e., food branch, food tree, food branch height) in the 1 minute interval, and ranged from 0 to 8 searches per individual. However, percentages were calculated for all minute intervals, regardless of the number of searches.

9.3 Results

For both species, observing a **conspecific** find the food cache led to significant changes in the pattern of their searching behaviour (Table 9.1). For *S. fuscicollis*, the proportion of searches on the food branch and at the branch height at which the food was found was significantly increased. However, they did not increase their proportion of searches in the food tree itself or their searching rate. For *S. labiatus*, the proportion of searches in the food tree and at the branch height at which the food was found was significantly increased. However, they did not increase the proportion of searches on the food branch itself or their searching rate. Indeed, they decreased significantly their search rate.

Table 9.1: Effect of a single food find by one individual on the searching pattern of its conspecific troop member, for *S. fuscicollis* and *S. labiatus* (pooling single-species and mixed-species troop data).

		Median % of searches at..		**Mean searching rate**
	food branch	**food tree**	**branch height**	
S. fuscicollis				
Before find (1 minute)	8.73	63.54	38.00	3.96
After find (1 minute)	46.03*	87.64	77.73*	3.85
S. labiatus				
Before find (1 minute)	10.36	55.71	36.25	3.40
After find (1 minute)	47.82	95.24*	76.54*	2.73*

* indicates a significant result

The response of both species to a food find by a **congener** was very different in that there were no significant changes in the pattern of their searching behaviour following such a find (Table 9.2). Nor did the monkeys alter their searching rate after a food find by a congener.

Table 9.2: Effect of a single food find by one individual on the searching pattern of its congeneric troop members, for *S. fuscicollis* and *S. labiatus*.

	food branch	**Median % of searches at.. food tree**	**branch height**	**Mean searching rate**
S. fuscicollis				
Before find (1 minute)	8.33	53.70	11.81	3.00
After find (1 minute)	21.25	88.97	45.05	2.59
S. labiatus				
Before find (1 minute)	23.48	70.45	40.91	3.25
After find (1 minute)	34.50	86.00	71.17	3.00

* indicates a significant result

The **finder** itself (*S. fuscicollis* or *S. labiatus*) did not significantly alter the pattern of its searching behaviour or its searching rate after a food find (Table 9.3). In the mixed-species troop test trials, *S. fuscicollis* found the food on 16 occasions and *S. labiatus* on 14.

Table 9.3: Effect of a single food find on the searching pattern of the finder, for *S. fuscicollis* and *S. labiatus* (pooling single-species and mixed-species troop data).

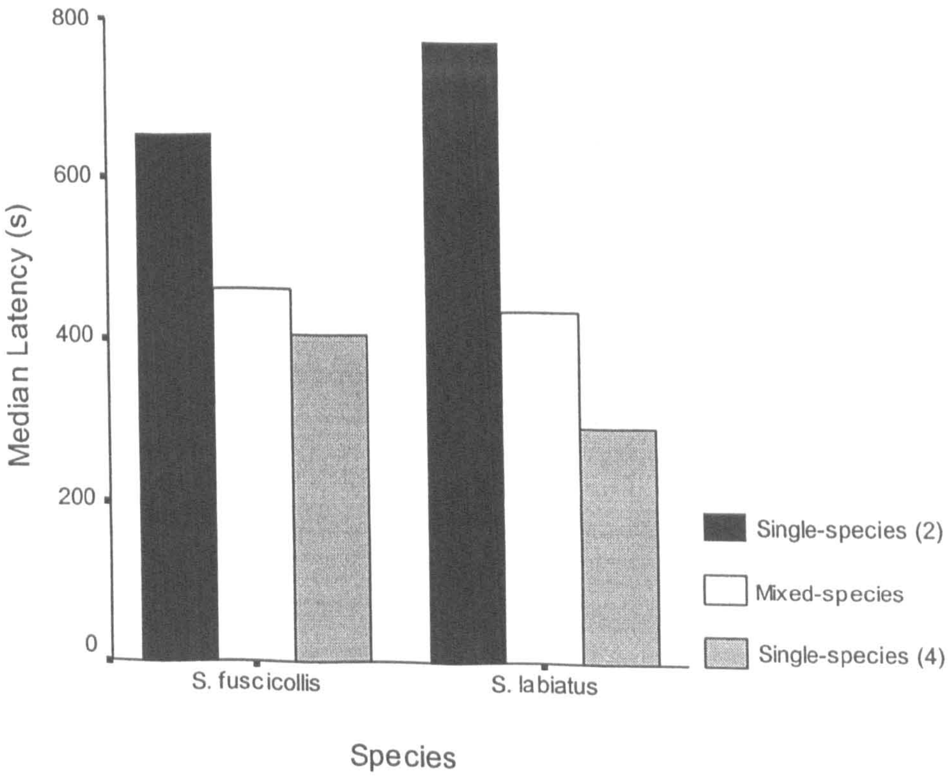
	food branch	**Median % of searches at.. food tree**	**branch height**	**Mean searching rate**
S. fuscicollis				
Before find (1 minute)	36.19	79.85	53.96	3.88
After find (1 minute)	21.98	89.00	76.78	2.13
S. labiatus				
Before find (1 minute)	41.47	74.78	61.10	3.39
After find (1 minute)	49.96	93.28	72.09	3.17

* indicates a significant result

Now considering the latency data, comparing the behaviour of each species separately in single- and mixed-species troops, it is found that both species were slower to find the food cache in single-species troops compared with either species in mixed-species troops (*S. fuscicollis*: $z = -2.60$, $n = 30$, $p < 0.05$; *S. labiatus*: $z = -2.69$, $n = 30$, $p < 0.05$;

Figure 9.1). This reduced latency to find the food in mixed-species troops may be due simply to the increase in the number of individuals in a mixed-species troop, rather than due to the propensities of congeners per se. To examine for this, the results for each species in the five mixed-species troops were compared with those from a single-species troop of each species (SF1 and SL1). No statistics were done due to the sample size. We can see from Figure 9.1 that both species are facilitated to find the food in the presence of a conspecific pair as well as in the presence of a congeneric pair. So the observed facilitation does appear to be simply a consequence of an increase in troop size from two to four individuals.

Figure 9.1: Median latencies (seconds) for *S. fuscicollis* and *S. labiatus* to find the food cache in single-species troops of two and four individuals and for either species in mixed-species troops.



Lastly, considering the number of food calls given by food finders during the 30 second period after the food find, there was no significant difference in the call rates of *S.*

fuscicollis or *S. labiatus* in single-species troops compared to either species in mixed-species troops.

Table 9.4: Mean (and median) call rates of food finders in single-species and in mixed-species troops.

Species	**Single-species troops**	**Mixed-species troops**	**Z value**
S. fuscicollis	1.83 (2)	1.25 (1)	$z = -1.68$, $p > 0.05$
S. labiatus	1.73 (2)	1.29 (1)	$z = -1.87$, $p > 0.05$

P-values refer to Mann-Whitney U test. Bold indicates a significant result.

9.4 Discussion

In the main, non-finders of both species did not alter their searching rates following finding of the food cache by a conspecific or congeneric troop-mate (although *S. labiatus* decreased its searching rate following a food find by a conspecific). This suggests that the monkeys were probably searching the cases at their maximum searching rate. This would indicate that the monkeys were highly motivated to search for the food cache; probably as a result of the training trials interspersed between subsequent test trials. Food finders of both species did not alter their searching rates following finding of the food either. Nor did they alter the pattern of their searching behaviour. So non-finders were not able to tell that the food finder had found food from these variables. However, all food-finders of both species gave food calls upon sighting the food, as has been the case in all experiments in this thesis. In fact, food calls appear to be an almost automatic response to sighting of food in both species. Although I did not measure recruitment directly, food calls appeared to be attractive in that non-finders quickly attended to the food finder following calling and usually quickly approached the finder. This same observation has been made elsewhere for captive *S. fuscicollis* (Menzel & Juno, 1985) and *S. labiatus* (Addington, 1992; Caine *et al.*, 1995). However, although food finders were joined by their conspecific and congeneric troop-mates, if a finder was joined at the food before it had consumed it all, it was generally unwilling to allow others to gain access to the food. Threats and mild agonistic behaviours, such as head-shakes, slaps, cuffs, lunges and open-mouth lunges, were directed at both conspecifics and congeners in defence of the food. This is likely to be because the food cache was a small, localised quantity of food, such that the finder considered it a monopoliseable resource. So being alerted to the location of the food cache did not result in opportunities to gain access to the food. If the food cache had been of greater quantity, then being alerted to its location would have probably resulted in access.

Under such circumstances, social foraging is advantageous, since being alerted to the location of food results in an increase in mean food intake. Being alerted to the location of food patches by other troop members is thus an advantage of social foraging. The advantages of foraging in a social troop that arise through local enhancement can be expected to increase with increasing troop size. As a direct consequence of individuals sharing information about discoveries of concealed food, increasing troop size can increase the rate at which patches of food are discovered. This was illustrated in this experiment by the fact that individuals of either species were quicker to find the food cache in mixed-species troops than in single-species troops. As described in the introduction to this chapter, such an effect will, in turn, result in an increase in individual mean rate of food intake and a decrease in the variance in this intake for troop members if food is not completely monopoliseable (Eisenberg *et al.*, 1972). Since an increase in troop size is a consequence of mixed-species troop formation, one might expect individual tamarins in wild mixed-species troops to increase their foraging efficiency in this way, especially given the patchy spatial and temporal distribution of their major food resources: ripe fruit and insects. However, probably as an adaptation to the extreme patchiness of their major foods, tamarins appear to exhibit advanced spatial mapping abilities (i.e., to hold in their spatial memory, information concerning the relative location of multiple food patches within their territory). Nevertheless, alerting other troop members to the location of food patches may increase foraging efficiency for the whole troop in addition to individual spatial knowledge. Yet, individual tamarins typically travel and forage in a cohesive unit. So it is perhaps unlikely that each has different knowledge about the location of food patches. However, associating species in mixed-species troops are less cohesive in that they segregate themselves vertically and progress through the forest in parallel but in separate strata. It is thus likely that each has have divergent knowledge about the location of food patches in these strata. Given that the species exhibit dietary overlap for their plant resources, in such situations, the foraging efficiency of individuals of one species will obviously be increased if they can join with the other species and capitalise upon the food finds of individuals of that species as well as those of their own. As long as food is on the whole clumped, and contains more than enough for individuals of both species, mixed-species groups may be mutually profitable.

As was mentioned in Chapters 2 and 7, Peres (1996) has shown that in mixed-species troops of *S. mystax* and *S. fuscicollis*, *S. mystax* are more often the first to encounter large productive feeding patches located higher in the forest (trees that can accommodate the whole mixed-species troop), whereas *S. fuscicollis* are more often the first to encounter smaller food patches lower in the forest. However, at the smaller food patches discovered by *S. fuscicollis*, *S. fuscicollis* are often displaced by the dominant *S. mystax*. A similar finding has been made for *S. fuscicollis*/*S. labiatus* troops, where *S. fuscicollis* are forced to wait until their congeners have finished eating before they can gain access to the resource (Hardie, 1998). Yet, since large non-monopoliseable patches account for a vast proportion of the tamarins' diets (Garber, 1993a; Peres, 1996), increments in feeding competition may not be large. So the opportunity to exploit each other's food finds at different heights may increase overall foraging efficiency (particularly for the congeners of *S. fuscicollis*). *S. fuscicollis* and *S. labiatus* do respond to each other's food calls (Prescott, pers. obs.), as they do alarm calls, and as we have seen in this experiment, they call as much in the presence of a congeneric pair as they do in the presence of a single conspecific.

Given that food calling is likely to decrease individual gain from a patch through increased feeding competition, especially at small patches and especially for subordinate *S. fuscicollis* in the presence of *S. labiatus*, why do tamarins almost invariably food call upon sight of food? Well, the cost of food calling in terms of feeding competition may be outweighed by kin selection benefits through sharing. Since tamarins typically live in related troops, replicas of an individual's genes will be present in other troop members. Callers may thus gain inclusive fitness payoffs in alerting conspecific troop members to the presence of food and sharing food with them. Or perhaps calling represents reciprocal altruism; where the cost of calling is outweighed by the prospect of future reciprocation regards alerting to the presence of food. However, in this experiment and others in this thesis, both species were observed to food call in response to small amounts of food (e.g., five mealworms). This finding corroborates that of Caine *et al.* (1995) and provides support for their suggestion for *S. labiatus* that food calls are not entirely governed by opportunities or inclinations to share food. The food items used in the majority of experiments in this thesis were highly preferred foods (e.g., mealworms, banana). We cannot rule out the possibility that food calls are a function simply of the arousal associated with seeing a quantity of preferred food (albeit a small quantity).

If the food is not shareable, and if the calls are not simply an automatic function of arousal, the question remains: why do food finders call since such an action is likely to lead to an increase in food competition? Again, the work of Caine *et al.* (1995) provides a possible reason in that they found *S. labiatus* food-finders to be sensitive to audience effects. That is, call rates were higher when a food-finder discovered food when its troop-mates were temporarily out of visual contact than when visible. This spatial-location effect led Caine *et al.* to suggest that food calling may ultimately benefit the caller by drawing its troop-mates near. For species in which individuals benefit from being in a group through reduced predation, there may be selection for isolated foragers to behave in ways that attract or recruit conspecifics to a food source (Lachlan *et al.*, 1998). Caine *et al.* suggest that, to the extent that tamarins are dependent upon intra-troop cohesion for critical daily activities and protection from predation, food calls may benefit the caller by drawing its allies near to maintain social contact for troop-mediated vigilance and other co-operative activities, even if calling leads to increased feeding competition (i.e., the costs of calling may be outweighed by the risks of being alone).

Even if food is small and cannot be shared, there may still be an advantage of being alerted to its location in that this may lead to learning about the type of place in which food can be found (i.e., influence non-finders to forage in such places). In this experiment, non-finders of both species responded to a successful food find by a conspecific by altering their searching behaviour to increase the proportion of searches in particular localities and as such, appeared to have learned something about the type of locality in which the food is to be found. *S. fuscicollis* increased their searching on the food branch and at the food branch height, whereas *S. labiatus* increased their searching in the same tree as the food branch and at the same height as the food branch. In terms of total distance, this represents a greater modification in searching behaviour for *S. labiatus* than for *S. fuscicollis*. This species difference in the response to a food find by a conspecific is perhaps a reflection of the different insect foraging strategies typically exhibited by these species in the wild (and to some extent in captivity). *S. fuscicollis* is an extractive forager and manually explores closed or concealing microhabitats (e.g., knotholes and crevices of trunks and branches) for wood boring or refusing insect prey. *S. fuscicollis* may have generalised to a more localised area than *S. labiatus* because their insect prey are relatively sedentary and probably occur in more localised patches then do the insect prey of *S. labiatus*. *S. labiatus* takes more mobile insect prey from the leaves and branches of the forest canopy using a highly visual stalk and pounce technique. Such prey are free to range over a wider area. This may account for the fact that *S. labiatus* did not increase their searching rate on the branch at which the food was found. Aside from responding to a food find by a conspecifc by searching in these localities, both species increased the proportion of their searches at the branch height at which the food was found. Provided food does reliably occur at the localities in which it was found, responding to the food finds of others by increasing one's search effort in the area in which the find was made will increase encounter rates with food. This may lead to an increase in mean intake rate and a reduction in the variance of this intake (i.e., increase foraging efficiency) in much the same way as does sharing the food find in the first instance.

Neither species altered their searching pattern after the finding of food by a congener. This result is strange given that, in all other experiments in this thesis, both species have been found to attend to the foraging behaviour of their congeners (and in so doing, have been found to learn from them). Since neither species responded to the food finds of their congeners by altering their searching behaviour in the manner they did to the food find of a conspecific, it cannot be concluded that mixed-species troops are advantageous to either in terms of learning about the *types* of location in which food is to be found. Nevertheless, as suggested by the latency data, as a result of sharing information about discoveries of food through food calls, an increase in troop size as a result of mixed-species troops formation can increase the rate at which patches of food are discovered by tamarins in their temporally and spatially uncertain environment. Provided there is enough food for individuals of both species, mixed-species troops may thereby increase foraging efficiency for both species.

9.5 Experiment 7: Local Enhancement when Foraging in Different Niches

Although the results are rather qualitative, the previous experiment demonstrated that both *S. fuscicollis* and *S. labiatus* are alerted to the location of a hidden food cache by the food calls of their conspecific and congeneric troop-mates. Non-finders respond to such calls by approaching the caller and, if the finder has not consumed all of the food, by attempting to gain some of it. However, there was a weakness in the experimental design of Experiment 6, namely that the two species were accustomed to foraging in exactly the same niche. We know that, in their natural environment, apart from when feeding on fruit, *S. fuscicollis* and *S. labiatus* habitually travel and forage in different niches, that is, at different heights in the forest (Yoneda, 1981, 1984a; Pook & Pook, 1982; Buchanan-Smith, 1990a, 1999). This vertical segregation is largely a consequence of adaptation to the separate strata in which their particular insects prey are found. Thus, Experiment 7 was designed to test whether, when accustomed to foraging in different niches (i.e., at different heights), the species continue to respond to the food finds of their congeners. If this were the case, one would predict that each species would spend a smaller proportion of their time searching in their own niche in mixed-species troops than in single-species troops.

The aim of the experiment was to investigate whether, when trained to forage in different niches, each species responds to the food finds of their congeners.

9.5.1 Study Animals

The study animals were eight of the troops tested as both single-species troops and mixed-species troops in Experiment 6 (see Section 9.2.1). Each was again tested in both single-species troops and mixed-species troops (SF3 & SL11, SF4 & SL4, SF5 & SL5, SF6 & SL6).

9.5.2 Design

The experimental design was broadly similar to that of Experiment 6. Each troop received two test trials, one as a single-species troop and one as a mixed-species troop, after a series of training trials. During the training trials, *S. fuscicollis* were trained to forage in the cases of the *lower* branches of the two trees in the 'End-Enclosure', and *S. labiatus* in the cases of the *upper* branches. This training was designed to produce a separation in foraging niche parallel to that observed in nature (although obviously not at the same absolute or relative heights). In the single-species troop test trial, the single-species troops searched the cases, none of which contained five mealworms. This test trial provided a baseline with which the monkeys searching after mixing could be compared. In the mixed-species troop test trial, the mixed-species troops searched the cases, one of which contained five mealworms. The location of this baited case (i.e., branch, tree, branch height) was counterbalanced between test trials and troops, such that, for two of the mixed-species troops it was located on the lower branches (the niche of *S. fuscicollis*), and for the other two it was located on the upper branches (the niche of *S. labiatus*). In addition to the training trials at the commencement of the experiment, troops received a single training trial between the single-species and mixed-species test trial. This served to maintain the monkeys' search effort during the second (mixed-species troop) test trial after mixing and, in this way, it is less likely that any modification in searching behaviour is a result of not being rewarded in the first (single-species troop) test trial. The experiment was conducted immediately after Experiment 6, between May and September, 1996, and May and August, 1997.

9.5.3 Procedure

The experimental procedure was similar to that Experiment 6 (see Section 9.2.4). No pre-training trials were required. Training and test trials were conducted in the 'End-Enclosure' before the tamarins' daily feed to ensure they were motivated to search for the food items.

(1) *Training Trials*

A mixed-species troop was moved to the 'End-Enclosure' and the two species each allowed to occupy one of the separate enclosures, C10 and C11, the outdoor portions of which adjoined the 'End-Enclosure' (see Figure 4.1). Each single-species troop then received six consecutive daily training trials before testing began, in which two mealworms were placed in all upper-branch cases for *S. labiatus* and all lower-branch cases for *S. fuscicollis*. The training consisted of releasing each species alternately into the 'End-Enclosure' to forage. Training trials lasted until 10 minutes after the last food item was found.

(2) *Test Trials*

Immediately following the sixth training trial, each single-species troop received the first test trial during which no cases contained mealworms. The testing procedure consisted of confining the monkeys indoors whilst all cases were cleaned free of debris and a fresh 2 cm layer of wood shavings placed in them. The monkeys were then released into the 'End-Enclosure' and permitted to search the cases under observation of the experimenter for 20 minutes (baseline). Immediately following this test trial, the single-species troops were isolated in their respective enclosures (C10 and C11). The following day each received a single training trial as in (1). Immediately following this training trial the single-species troops were isolated in the indoor portion of one of the respective enclosures and thereby re-mixed to form a mixed-species troop of four individuals. The mixed-species troops were then released into the 'End-Enclosure' for the mixed-species troop test trial, the procedure for which was as in '*Test Trials*', Section 9.2.4. All four mixed-species troops found food in the first 5 minutes of the test trials. Mixed-species troop test trials lasted until 20 minutes after the food was found.

9.5.4 Recording Methods

Recording methods were exactly as in Experiment 6 (see 9.2.5).

9.5.5 Data Analysis

For the mixed-species troop test trials in which the food was located in the lower branches (the niche of *S. fuscicollis*), *S. fuscicollis* found the food. For the mixed-species troop test trials in which the food was located in the upper branches (the niche of *S. labiatus*), *S. labiatus* found the food. Therefore, the percentage of searches within their 'own' niche when in single-species troops was compared with that when in a mixed-species troops before and after a food find by a congener in its niche for each species separately using the Mann-Whitney U test (although, the single- and mixed-species troop data sets were not wholly independent)[1]. Significance was set at alpha < 0.05.

9.6 Results

Comparing the percentage of searches in their own niche in single-species troops with that before the food find in mixed-species troops, it is found that both species spent the same proportion of their time searching in their own niche when in mixed-species troops as they did in single-species troops (*S. fuscicollis*: $z = -0.88$, $n = 4$, $p > 0.05$; *S. labiatus*, $z = -0.44$, $n = 4$, $p > 0.05$; Table 9.5).

Comparing the percentage of searches in their own niche in single-species troops with that for the first 5 minutes after the food find in mixed-species troops, it is found that both species spent the same proportion of their time searching in their own niche following a food find by a congener when in mixed-species troops as they did in single-species troops (*S. fuscicollis*: $z = -0.29$, $n = 4$, $p > 0.05$; *S. labiatus*, $z = -1.02$, $n = 4$, $p > 0.05$). Comparing the percentage of searches in their own niche in single-species troops with that for the full 20 minutes after the food find in mixed-species troops, again, it is found that both species spent the same proportion of their time searching in their own niche following a food find by a congener when in mixed-species troops as they did in single-species troops (*S. fuscicollis*: $z = -1.44$, $n = 4$, $p > 0.05$; *S. labiatus*, $z = -0.58$, $n = 4$, $p > 0.05$).

---

[1] Note that before the food find in mixed-species troops constitutes a maximum of five minutes searching time. Single-species troops, and after the food find in mixed-species troops, constitute 20 minutes searching time. Therefore, comparisons are made for the first 5 minutes after the food find as well as for the full 20 minutes after the food find. The actual number of searches on which the percentages for each individual are based are variable, the range being 5 to 42.

Table 9.5: Median percentage of searches by each species which were in their own niche in single-species troops, and in mixed-species troops before and after a food find by a congener in its niche.

	***S. fuscicollis* (lower cases)**	***S. labiatus* (upper cases)**
Single-species troops	14.0	28.5
Before the food find in mixed-species troops	27.5	28.0
The first 5 minutes after the food find in mixed-species troops	24.5	20.0
The full 20 minutes after the food find in mixed-species troops	28.5	27.5

* indicates a significant result at the $p < 0.05$ level for the Mann-Whitney U test.

9.7 Discussion

As detailed in Chapter 7, for wild tamarin mixed-species troops, food patches which are quite accessible may occur at heights not normally inspected by members of one particular species. For example, Peres (1996) writes that

> "*while they [Urucu tamarins] shared a congruent home range, the location of food sources was unlikely to be* "presumably well known to both" *because of the marked vertical stratification they presented*" (p. 719).

By chance, individual *S. fuscicollis* should encounter more understory patches and their congeners more midstory or understory patches, regardless of whether they rely upon cognitive abilities to locate patches or chance encounters. It may be possible for associating species to increase their foraging efficiency by combining the separate searching skills of the different species in the separate strata and thereby increase the total scanning range of the whole troop. As long as food is on the whole clumped and a patch contains more than enough food for each individual, mixed-troops will be profitable. In this experiment, both species showed virtually no change in search effort in their own niche following mixing into a mixed-species troop for before or after a food find by a congener in its niche. Thus, it cannot be concluded that, when trained to forage primarily in different niches, the species continue to respond to each other's food finds by concentrating their searching in the niche in which the food was found. So again, as in Experiment 6, the species did not appear to learn from their congeners information about the *type* of location in which food can be found. This is perhaps due to the fact that the experiment more closely mimicked conditions for insect foraging rather than fruit foraging. Since the two species exhibit different insect foraging strategies and take different insect prey in the wild, perhaps this is why they did not respond to the food find of their congeners by increasing their search effort in the area of the find in this experiment nor in Experiment 6. Anecdotally, they did however attend to the food calls of finders and approached the finders at the food source, but since recruitment was not measured directly, this cannot be analysed quantitatively.

9.8 Conclusion

In species that derive fitness benefits from aggregation (e.g., increased predator detection and avoidance), foraging information may be transmitted between individuals by processes as simple as following conspecifics (and thereby being exposed to the same aspects of the environment as they are) (Laland & Williams, 1997). *S. fuscicollis* and *S. labiatus* food finders were found to alert conspecifics and congeners to the presence and location of food with food calls. Qualitatively, non-finders responded to these calls by approaching the food finder at the food source probably for the opportunity to gain access to the food. An increase in troop size, as a result of mixed-species troop formation, would increase the rate of food finding and may thereby lead to an increase in mean rate of food intake and a reduction in the variance of this intake for troop members. Provided there is enough food for individuals of both species, mixed-species troops may thereby increase foraging efficiency for both species. The cost of calling to the caller, in terms of increased feeding competition, may be outweighed by benefits accrued through sharing via kin-selection or reciprocal altruism. Even if food is not shared, callers may benefit by drawing their troop-mates near in order to maintain vigilance and other co-operative activities.

Not only can the foraging behaviour (food calls) of other troop members increase foraging efficiency by alerting individuals to the general locations in which food is located, but furthermore, once within the vicinity of the food, foraging individuals can learn about the types/nature of locations that are likely to contain food. This too may increase foraging efficiency in much the same way as does sharing in the first instance. Conspecifics were found to learn from each other in this way but congeners were not, so we cannot conclude that mixed-species troop formation is an advantage in this way.

Chapter 10

Social Learning About Food Patch Quality

"A fundamental problem for any animal is finding food. Many animals solve this problem with a good memory and an appropriate food-searching strategy. The memory provides information about places that have been visited previously and the results of those visits. The strategy takes this information and directs subsequent searches to the most profitable areas, maximizing the benefits and minimizing the costs."

[Olton, 1982: p. 205]

10.1 Introduction

Most optimal foraging models conceptualise foraging behaviour as consisting of a series of decisions between alternatives made on the basis of the rate of energy or nutrient intake that each alternative could be expected to produce relative to any costs (e.g., from exploration and travel, or from predation). These decisions require the foraging animal to possess, remember and integrate information about its environment. The optimal foraging animal must know the characteristics of the plant and animal prey it consumes, where this prey is likely to be located and when it is available. For animals whose prey occurs in patches (i.e., discrete areas within the habitat having a greater density of prey than the habitat as a whole), optimal foraging also involves knowing the density of prey in multiple patches (i.e., the reward value or quality of each patch) and the temporal availability of prey within these patches, so that as a patch becomes depleted they can successfully exploit other patches. In fact, it has been suggested that information concerning: (a) the location and distribution of multiple food patches; (b) the distances between these patches; (c) the rates of resource renewal and food capture within them; and (d) any differences in the productivity of individual feeding trees within patches is retained by animals and used in their feeding decisions (e.g., Altmann, 1974; Orians, 1981; Kamil & Yoerg, 1982; Real *et al.*, 1982; Cant & Temerin, 1984; Krebs & McCleery, 1984; Pyke, 1984; Kagel *et al.*, 1986; Robinson, 1986).

In the case of frugivorous arboreal rain forest primates, such information is of particular importance. Tropical rain forests are generally characterised by high tree species diversity and low average species density (generally less than one tree of a given species per hectare), with the majority of tree species distributed in small, widely scattered patches (e.g., Chivers, 1977; Hubbell, 1979; Estrada, 1984; Robinson, 1986; Milton, 1988). Few species exhibit a random or uniform distribution. In addition, the fruiting and flowering schedules of tropical trees may vary on a time scale measured in months (analogous to fruiting phenology), days (analogous to fruiting rates) or even a few hours (analogous to rates of nectar renewal in some flowers). Furthermore, the denseness of the canopy often reduces the effectiveness of visual cues beyond a distance of some 10 - 15 metres (Garber, 1989). These factors place strong constraints on the efficiency with which arboreal rain forest primates can find particular feeding sites and tamarins are no exception. Due to their small body size, high metabolic rate, limited gut volume and rapid rate of food passage (Crandlemire-Sacco, 1986; Garber, 1986), they require a diet high in nutrient quality and available energy (Garber, 1989). These demands are met by consuming primarily ripe fruit and insects (along with plant exudates, nectar and small vertebrates). However, the fruit resources taken by tamarins are characterised by a scattered and patchy distribution and the production of small amounts of ripe fruit each day (Crandlemire-Sacco, 1986; Garber, 1986, 1989; Soini, 1987; Terborgh, 1983, 1986). In addition, as described in Chapter 9, they can exhibit pronounced inter-specific and intra-specific fruiting asynchrony such that it is difficult to predict when a particular species, tree or patch of trees is about to fruit

(Peres, 1993b, 1996). Such unpredictability in the spatial and temporal distribution and availability of their fruit resources is likely to have a major impact upon tamarins' foraging decisions. With this background, the energetic cost of choosing to forage in a depleted patch, or of using inefficient or incorrect (less than optimal) travel routes, is likely to be very high. The ability to retain and integrate information concerning the locations, rates of renewal, and food rewards of patchily distributed fruit resources is thus likely to be critical for their foraging success (Garber, 1987, 1988b, 1989).

Insects, like plants, also exhibit complex patterns of distribution in time. Relative to fruit, which although scattered in distribution is concentrated in discrete patches, insects are more diffuse in the environment, dispersed and hidden. However, their spatial distribution is linked to their particular plant prey or reproductive host species. Links between insect life history and the availability of particular plant phases, together with the strong influence of climate, mean also that insect communities may undergo drastic changes in abundance, diversity and taxonomic composition in tropical rain forests in concert with the annual cycle of seasons (Janzen, 1973; Smythe, 1974; Ricklefs, 1975). Moreover, diurnal changes in ambient light or temperature regime can have pronounced effects on the temporal and micro-spatial distribution of insect prey (or on the susceptibility to capture of such prey) (Terborgh, 1983). This variation in the daily and seasonal availability, spatial distribution and habitat location of insect prey is also likely to have a major impact on tamarin foraging decisions and foraging success (Garber, 1993b). In order to forage efficiently, one would expect tamarins to acquire information pertaining to this spatial and temporal variation in the distribution of their major food resources, and to adopt appropriate foraging strategies in response. The information upon which these strategies are based is acquired during a process of exploration and sampling.

Information Acquisition and Sampling

Optimal foraging in animals reliant upon patchily distributed resources is dependent upon the ability to remember and integrate various classes of patch information necessary for use in foraging decisions. However, individual foragers are unlikely to have perfect knowledge concerning this information, as a consequence of an imperfect ability to gather, store and recall such information (e.g., Smith & Sweatman, 1974; Gill & Wolf, 1977; Pyke *et al.*, 1977), but also as a consequence of variability in their foraging environment (e.g., Post, 1984; Pyke, 1984). Therefore, it has been suggested that, in a changing world, foraging animals should devote time to *sampling* their environment in order to obtain and update foraging information for use in subsequent foraging decisions (e.g., Royama, 1970; Krebs *et al.*, 1974; Smith & Sweatman, 1974; Zach & Falls, 1976; Stephens & Charnov, 1982). If they have the ability to profit from past experience, then they can improve their foraging efficiency by recalling appropriate responses to information gained through sampling and by changing their foraging behaviour accordingly. For example, Royama (1970) argues that it is important for animals to feed in "profitable" feeding areas, defined as the amount (biomass) of food the predator can collect for a given amount of hunting effort (time spent hunting). He suggests that, in order to maximise their foraging efficiency, they should sample food patches in different parts of their habitat, to assess patch quality, and then alter their foraging behaviour according to the reward value of the different patches, spending the most time where the success rate is highest.

The ability of animals to make systematic choices of foraging areas has been tested in several laboratory and field experiments (e.g., Goss-Custard, 1970; Smith & Dawkins, 1971; Smith & Sweatman, 1974). In Smith and Dawkins' (1971) experiment, individual *P.*

major were found to combine learning within patch sampling to maximise their searching efforts with four food patches varying in prey density (1, 4, 8, or 16 mealworms per site). The birds allocated their search time to match approximately the rewards of the four patches. When the patches were exchanged (those that previously had the highest prey density became the lowest and vice versa), the birds continued to visit the patch that had previously been the most profitable, but over several trials began to concentrate on the new best patch, substantiating a learned assessment of the quality of different spatial areas. Through sampling, the birds were able to determine if the patch they were currently using still had a higher density of resources than the other patches, and if not, change their behaviour accordingly. Pyke (1984) writes that

> *"if the relative quality of two food patches switches from time to time, then an animal that can feed in either patch should always spend some time in what at the time might be the worst patch so that it could make appropriate adjustments when conditions change"* (p. 528).

Pyke also reports experiments in which birds did not spend all their foraging time on patches with the greatest abundance, but regularly probed other patches to assess patch quality (Pyke, 1981). Smith and Sweatman (1974) suggest that such sampling behaviour represents a long-term (as opposed to a short-term) adaptation to a fluctuating environment. If the natural environment of an animal undergoes fluctuations such that food patches which have high food abundance at one time have low food abundance at a later time, and vice-versa, then the short-term foraging strategy of allocating all available time to the best patch would not be as adaptive as the long-term strategy of sampling all patches in order to continually track food abundance.

Thus foraging animals appear to make assessments of food patch quality and to monitor patches in order to forage efficiently. It is thought that they combine past experience, including a knowledge of the distribution of resources among patches in the environment, with current patch sampling information to estimate patch quality (e.g., Oaten, 1977; McNamara & Houston, 1980; Iwasa *et al.*, 1981; McNamara, 1982; Cuthill *et al.*, 1990; Valone, 1991, 1992). However, despite the growing body of theoretical and empirical studies addressing the question of how solitary foragers obtain estimates of patch quality, few studies to date have considered the possibility that the process(es) of patch quality estimation may differ in group foraging animals. Exceptions include the work of Valone (1989, 1991) and Valone and Giraldeau (1993) who point out that group foragers actually have access to three sources of patch information ('patch sample information', 'pre-harvest information' and 'public information'), the third of which solitary foragers do not have access to. Patch sample information is that accumulated during patch use and includes the time spent in a patch, the number of resource items obtained in it, and the time since the last resource capture. Pre-harvest information includes prior information about the distribution of resource patches in the environment (McNamara & Houston, 1980), sensory information (e.g., visual or olfactory information) (Valone & Brown, 1989), and memory of regularly renewing patches (Valone, 1991) or environmental cues that indicate patch quality (Mitchell, 1989). Public information is that acquired by gathering information on the foraging success of other group members in food patches.

As social foragers, individual tamarins might be expected to benefit from public information, taking advantage of the collective patch quality assessments of their troop-mates, in addition to their own assessments. In this way, social learning would allow them to track environmental variability more efficiently than would asocial learning alone, as social learners can quickly and safely home in on appropriate behaviour by sharing up to date foraging information (Laland *et al.*, 1993). Such an advantage applies particularly to species whose food occurs in small, highly localised patches (ripe fruit) or for which the abundance of different food types changes from place to place in a relatively small area (insects). Mixed-species troop formation, by increasing troop size, may therefore increase the foraging efficiency of individual tamarins since sources of patch information will be more numerous, particularly for shared fruit resources. The advantage need not be precluded by the vertical segregation between associating species. As long as the patch is non-monopoliseable, then individuals of either species may still benefit from not having to make patch quality assessments based simply on their own sampling experience.

Before investigating increased foraging efficiency through transfer of patch quality information between individual tamarins, it is first necessary to demonstrate that individuals can recognise and discriminate between patches of different quality, and having acquired this information, use it to increase their foraging efficiency. Experiment 8 was devised, loosely based upon the laboratory experiments reviewed above investigating the ability of birds to make systematic choices of foraging areas. Free-ranging single-species pairs of *S. fuscicollis* and *S. labiatus* were required to search for aggregations of food items located in four discrete patches. Manipulation of the density of food in the different patches enabled me to determine whether foraging individuals discriminate between profitable and less-profitable areas, and henceforth, whether they distribute their search effort in relation to spatial differences in the quality of feeding patches (i.e., whether they specialise on the rich patches containing a high density of food) and how fast and how strongly they specialise.

Subsequently, Experiment 9 was designed to investigate the extent and way in which cognition and spatial memory are involved in this specialisation. The density of food in the different patches was switched such that what was once the most profitable patch became the least profitable and vice versa. This enabled me to investigate how well the tamarins maintain their foraging efficiency when preferred feeding patches become unprofitable (the way in which they respond to variations in the temporal and spatial distribution of their food being important in helping to understand how their behaviour is adapted to ensure efficient foraging generally). In addition, since the switch in food density was visually cued for half the pairs tested but not the other half, the experiment enabled me to determine to what extent spatial memory and visual cue associative learning aid in responding to such a change.

Experiment 10 investigated inter-specific social learning of patch quality information. Previous experiments (in Chapters 5 and 6) have shown that associating species in tamarin mixed-species troops are capable of learning from each other about various classes of food-related information. Therefore, as social foragers, one might expect individual tamarins to attend to the behaviour of their conspecific and congeneric troop-mates and to take advantage of their knowledge about the distribution of food patches within the environment and variation in the density of food within these (public information). Knowing that other troop members (species) are doing well in a patch may enable individual animals to estimate patch quality more rapidly and accurately and thereby forage more efficiently.

10.2 Experiment 8: Response to Spatial Variation in Food Patch Quality

The aim of the experiment was to investigate the ability of pairs of individuals of S. fuscicollis *and* S. labiatus *to discriminate between high quality (prey-dense) and low quality (less prey- dense) food patches, and henceforth, whether they distribute their* *search effort in relation to differences in the quality of the food patches. Furthermore, the experimental design enabled me to examine whether the opportunity to use local visual associative cues indicating patch quality aided in this process.*

10.2.1 Study Animals

The study animals were four adult male-female pairs of *S. fuscicollis* (SF3, SF6: Table 4.1; SF7, SF9: Table 4.3) and four of *S. labiatus* (SL3, SL6: Table 4.2; SL7, SL9: Table 4.4). At any one time, one pair of each species occupied separate enclosures adjacent to the 'Free-Range Area'. Further details of housing and husbandry are given in Chapter 4 (Section 4.6). The monkeys' ages were similar across species and ranged from 1 year 6 months to 10 years 3 months at the time of testing. Normally maintained as mixed-species troops (SF3 & SL3; SF6 & SL6; SF7 & SL7; SF9 & SL9), the troops were separated into single-species pairs only when necessary according to experimental protocol. The female *S. labiatus* from SL6 was heavily pregnant during testing.

10.2.2 Design

Experiments 8, 9 and 10 were conducted in the 'Free-Range Area' of the old zoo (see Section 4.6.3). Four discrete foraging patches, located in four separate trees between 5 and 7 metres apart, were created in the wooded part of this area. Each patch consisted of twenty cylindrical, black-plastic camera-film cases (as used in Experiments 6 and 7; hereafter referred to simply as 'cases') attached to four branches in the tree (five cases per branch) (Plate 13). The cases were attached to the branches with garden wire and were positioned approximately 20 cm apart. The branches chosen to support cases were approximately 30 cm apart vertically, and formed part of a 'branch cluster' within each

Plate 13: A foraging patch within the wooded 'Free-Range Area'.

Plate 14: *S. labiatus* searching the cases of a high quality patch (as indicated by the red-ribbons.

tree. The branch clusters were matched as closely as possible for height (the branches in each ranged from 1.5 to 2 metres above the ground), branch size and orientation, exposure and distance from the home enclosures. Patches were labelled, north to south, A, B, C, and D, and the branches and cases were given codes to aid data recording. (e.g., 'Au2' denoted patch 'A', 'upper' branch, case number 2).

At any one time, a single-species pair of each species occupied the two enclosures adjacent to the 'Free-Range Area'. Each pair [1] was released separately into the wooded part of the 'Free-Range Area' to forage in the four patches of twenty cases in which 0, 5, 10 and 15 food items were placed. Within each patch, the position of food items was randomised using random number tables, but with the restriction that no case was allocated more than one food item. A 2 cm layer of wood shavings was placed on top of the food items and in all other cases. As for Experiments 6 and 7, the fact that all cases contained wood shavings meant that the monkeys could not tell which of the cases contained food simply by scanning from above. Instead, in order to see if a case contained food, it was necessary for the monkeys to approach the case, flick out most of the wood shavings with their hands, and rake through the remainder.

Each single-species pair received ten test trials, one per day, and each the opposite distribution of prey density per patch to their congeners (see Table 10.1) (e.g., if SF3 was presented with 0, 10, 5 and 15 food items in patches A, B, C and D, then SL3 was

---

[1] I chose to test the monkeys in pairs to minimise the stress of separation and to preserve as much of their natural foraging behaviour as possible. Moreover, testing in pairs provided simultaneous information on two individuals and yielded inductive data on the social dynamics of food discovery. However, because the study animals were not tested individually it is likely that each did not experience exactly the same prey density distribution. In attempt to control for this, I endeavoured to ensure an adequate number of trials, with an adequate number of prey items, in order that each individual may experience, and have the opportunity to learn, as similar a distribution as possible before becoming satiated.

Table 10.1: Change in the distribution of prey density in patches A, B, C and D from Experiment 8 to Experiment 9 for single-species pairs tested in the presence and absence of cues.

	SF3	**SL3**	**SF6**	**SL6**	**SF7**	**SL7**	**SF9**	**SL9**
Experiment 8 (trials 1-10)	0, 10, 5, 15	15, 5, 10, 0	15, 5, 10, 0	0, 10, 5, 15	0, 10, 5, 15	15, 5, 10, 0	15, 5, 10, 0	0, 10, 5, 15
	↓	↓	↓	↓	↓	↓	↓	↓
Experiment 9 (trials 11-20)	15, 5, 10, 0	0, 10, 5, 15	0, 10, 5, 15	15, 5, 10, 0	15, 5, 10, 0	0, 10, 5, 15	0, 10, 5, 15	15, 5, 10, 0
Cues present?	no	no	no	no	yes	yes	yes	yes

presented with 15, 5, 10 and 0 items in patches A, B, C and D). The significance of this shall become clear in Experiment 10 (Section 10.8).

The quantity of food in each patch was counterbalanced between and within species for the eight pairs tested in an attempt to check for preferences for particular patch locations. The monkeys were required to learn to associate a particular patch location with a particular prey density (i.e., to encode and associate spatial and patch quantity information that could be used to distinguish one patch from another, and then distinguish between the four patches). In accordance with mainstream optimal foraging theory, I assumed that the monkeys were acting to maximise their net rate of energy intake in their foraging [1].

The experiment was conducted between June and August, 1996 (SF3 & SL3, SF6 & SL6), and between May and July, 1997 (SF7 & SL7, SF9 & SL9). For SF7 and SL7, and SF9 and SL9, tested during the second summer of data collection, the experiment was carried out as described above, except that patch quality was visually-cued such that the patches containing 15 and 10 items were marked by the presence of five red ribbons within each patch (Plate 14). The fact that, for half the pairs, patch quality was cued, and for the other half it was not, enabled me to investigate how spatial memory and visual associative

---

[1] Although I assumed that the monkeys were acting to maximise their net rate of energy intake in their foraging, it is unlikely that they were under great pressure to do so, due to both over-provisioning of their daily rations and due to the fact that the experimental food patches were relatively close together (each was 5 - 7 m apart). This meant that the cost in time and energy of visiting a poor patch was probably negligible. However, the monkeys were highly motivated to search for the preferred, protein-rich mealworms at the time of day the experiment was conducted, and individuals appeared to compete with one another in order to acquire as many as possible. Due to the limited number of baited cases within each patch, each visit to an empty case will have significantly decreased an individual's chance of discovering baited cases not already depleted by its conspecific pair-mate. Thus the presence of another, simultaneously exploiting the same patches, is likely to have increased the cost of foraging within a poor quality patch and may have provided a strong enough incentive to learn which patches contain the most baited cases and to concentrate search effort upon these.

cue learning aid in responding to environmental change. This issue is investigated briefly in this experiment and in more detail in Experiment 9.

10.2.3 Procedure

(1) *Habituation*

All pairs had been housed as mixed-species troops prior to experimentation and were easy to separate into single species pairs for the duration of the experiment. Pairs unfamiliar with the enclosures adjacent to the 'Free-Range Area' experienced an initial two week habituation period to the enclosures before release. There then followed a two week habituation period to the 'Free-Range Area' itself, following the initial release, during which the monkeys familiarised themselves with the 60 metre by 40 metre wooded and turfed area. During this second week, records of 1 m^2 quadrat use in the area were collected and later reviewed to ensure the tamarins exhibited no pre-existing preferences for one or other of the trees chosen to contain the different feeding patches.

(2) *Training Trials*

Prior to testing, pairs were trained to search for mealworms in ten cases attached to random branches in their enclosure, two mealworms having been concealed beneath a 2 cm layer of wood-shavings in all cases. Twice-daily training trials of 20 minutes were given until it was observed that all individuals had learned to forage for the food items in this manner. The cases were present in the enclosures only during the 20 minute training trials.

(3) *Test Trials*

Eighty cases were positioned in the four patches (twenty in each patch) before the experimentation period began but after habituation to the 'Free-Range Area'. Test trials were given daily (unless the weather was particularly inclement), and always commenced between 0900 and 1200 hours. The tamarins on the 'Free-Range Area' were always fed their normal diet between 1200 and 1300 hours and testing before their daily feed meant that, apart from overnight access to the previous day's remainder, the tamarins had not eaten on the day of testing and were thus particularly attentive to, and motivated to forage for, the mealworms.

In order that I could set out the appropriate ratio of rewarded to unrewarded cases in each patch without the tamarins observing, it was necessary to first tempt the monkeys into their enclosures with pieces of fresh fruit and contain them there. The cases were then loaded with mealworms and wood shavings. Recording began the moment the access-hatch to 'Free-Range Area' was opened (via a wire pulley), and the single-species pair to be tested released onto the 'Free-range Area' in order to forage in the patches. Whilst the test pair were foraging, the non-test pair were contained within their enclosure to prevent any possibility of observational learning (it was not possible to view the feeding patches in the 'Free-Range Area' from the adjacent enclosures due to obstruction by foliage).

Test trials lasted from the time the troop entered the 'Free-Range Area' to until 5 minutes after the last case visit (cessation of searching by the last individual). Individuals usually remained in close association and thus entered the wooded area with, at most, 10 seconds of each other. The monkeys usually searched persistently and exhaustively within each patch, except in trials disrupted by bad weather, and moved from one patch to another very quickly. Following the test trial, the pair were again contained in their enclosure and the cases cleaned ready for the following trial.

10.2.4 Recording Methods

The sampling strategy was all-occurrences sampling (Altmann, 1974). Standing approximately 5 metres from the foraging monkeys, and with occasional, minimal shifts of position, I was able to observe the behaviour of the pair simultaneously. In order to ensure that my presence did not influence patch choice, I stood in a position equidistant from the four patches. The study animals were well-habituated to my presence in the wooded area and paid me no concern. I dictated into a miniature tape recorder a verbal record of all instances in which an individual visited a particular case. Visits were classified as either looks (i.e., the animal peered into the case but did not insert its hands into the case) or searches (i.e., the animal actively manipulated the wood shavings, cupping them or flicking them out of the case, in order to see if a food item was concealed beneath them). The time spent searching each case was not recorded, but the time at which each individual ceased and resumed searching was. In addition, I recorded each time a food item was found and eaten and by whom, each time an individual entered and exited a patch (i.e., approached within and exited outwith 15 cm of a case), and any calls and competitive interactions (food stealing, agonistic behaviour and displacements: see Table 4.5) together with the identity of the actor and receiver. Data from the audio-tapes were transcribed onto record sheets.

10.2.5 Data Analysis

From the data collected it was possible to calculate, for each individual in each patch the number of searches per patch, the number of successful searches ('captures') per patch, the foraging efficiency per patch (i.e., number of successful searches per patch / number of searches per patch), and the frequency and direction of competitive behaviours. A number of variables were calculated because of the difficulty in analysing records of real free-foraging behaviour.

The data were split into two blocks (the first five trials and second five trials) and non-cued and cued individuals analysed separately for differences in the number of searches and foraging efficiency for trial block and for prey density using the Repeated Measures ANOVA. Significance was set at alpha < 0.05. Competitive interactions were so few as to not warrant analysis.

10.3 Results

Results are presented for the non-cued and cued individuals separately. A Repeated Measures ANOVA, pooling species, revealed no main effect for species for either the number of searches or foraging efficiency for non-cued and cued individuals (Table 10.2), Consequently, the results presented below are for the data set pooled for species.

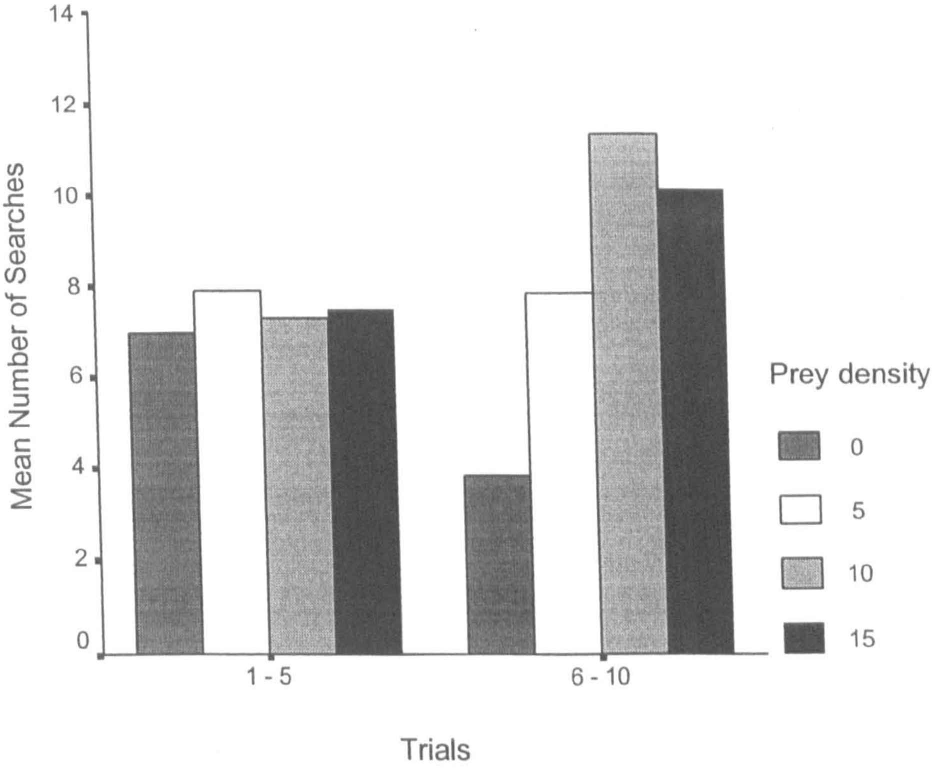
Table 10.2: Repeated Measures ANOVA F-values and mean scores for species differences in the mean number of searches and mean foraging efficiency by cued and non-cued individuals.

Individuals	**Variable**	**Species (*S. fuscicollis* / *S. labiatus*)**
Cued	Number of searches	$F_{1,37} = 0.001$, $p > 0.05$ (8.24, 8.22)
	Foraging efficiency	$F_{1,37} = 3.90$, $p > 0.05$ (0.31, 0.26)
Non-cued	Number of searches	$F_{1,38} = 1.28$, $p > 0.05$ (7.95, 7.33)
	Foraging efficiency	$F_{1,33} = 0.16$, $p > 0.05$ (0.25, 0.26)

<u>Non-cued Individuals</u>

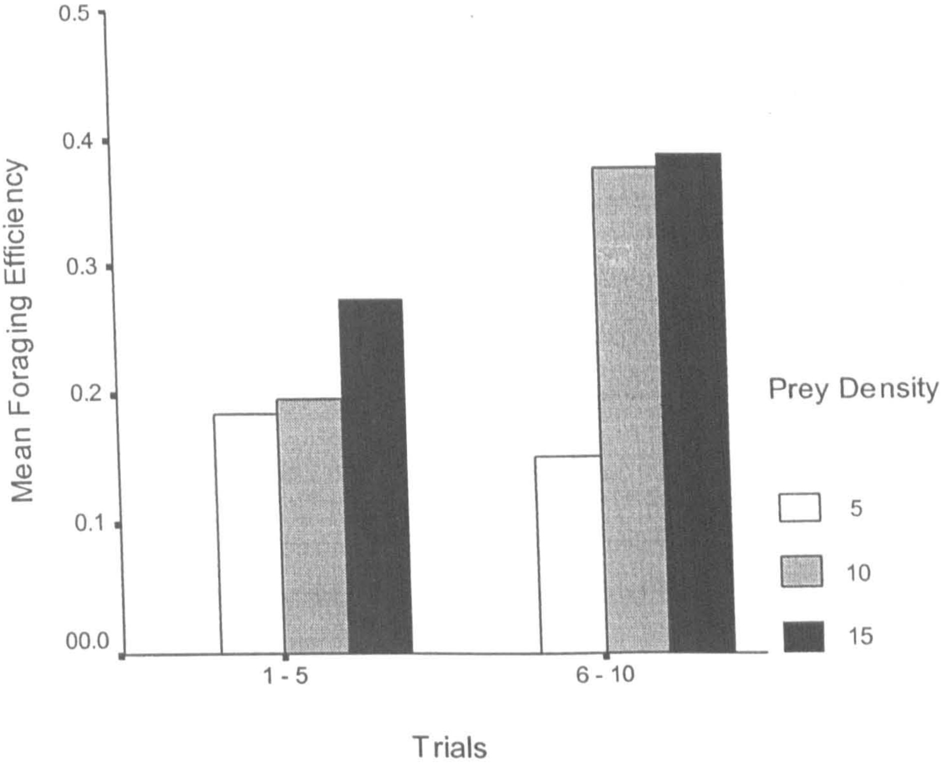
Considering the number of searches performed by non-cued individuals first, there was no significant effect for trial block, so the number of searches (over all patches) did not differ in the second block of trials (6 - 10) compared to the first (1 - 5) ($F_{1,39} = 0.88$, $p > 0.05$; Figure 10.1). However, there was a significant effect for prey density ($F_{3,117} = 15.69$, $p < 0.05$) and a significant interaction between prey density and trial block ($F_{3,117} = 7.75$, $p < 0.05$). In the first block of five trials, searching appeared random across the four prey densities. By the second block of five trials, searching is non-random, with a strong concentration of searching at the higher densities. So the monkeys appeared to respond to the difference in prey density in the different patches by concentrating their search effort on the most prey-dense patches and by decreasing their search effort on the patch containing no food items. In fact two thirds of the monkeys' search effort was concentrated on the more profitable patches containing 10 and 15 food items per patch, and only one third of their search effort on the less profitable patches containing 0 and 5 food items per patch. However, although there was a clear tendency for the monkeys to search selectively at higher prey densities, there was no simple ranking of search effort in proportion to prey density: more searches were conducted at density 10 than 15.

Figure 10.1: Mean number of searches at different prey densities for non-cued individuals (pooling species).



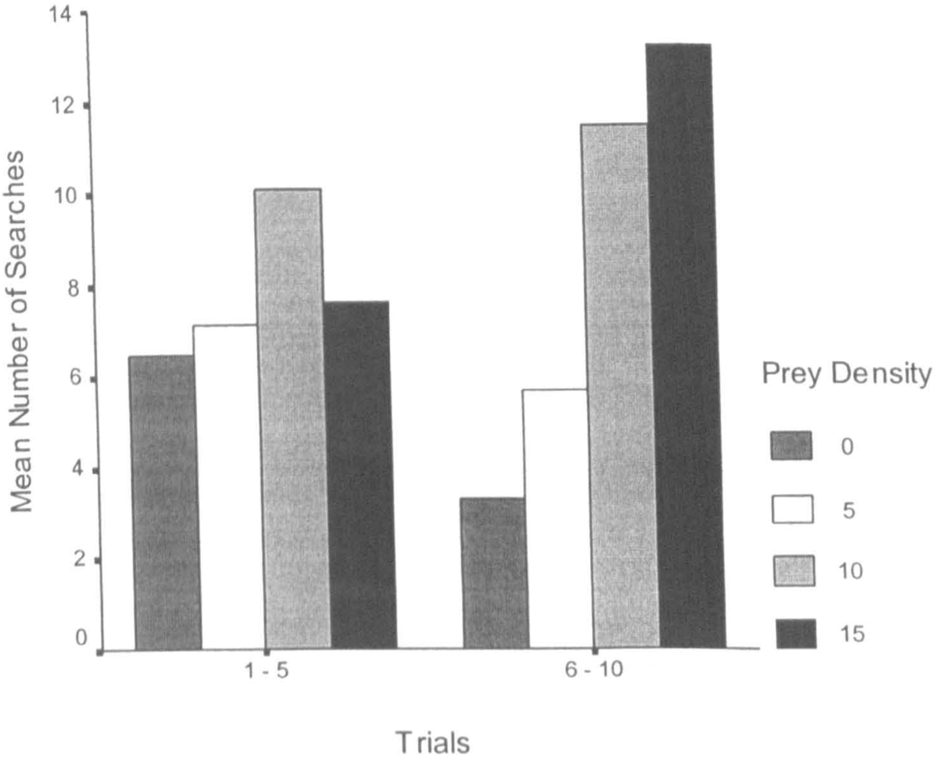
What is the consequence of this concentration of search effort on the higher prey densities for foraging efficiency? There was no significant effect for prey density ($F_{2, 68} = 2.29$, $p > 0.05$), but a significant effect for trial block ($F_{1, 34} = 10.911$, $p < 0.05$) and a significant interaction between prey density and trial block ($F_{2, 68} = 6.84$, $p < 0.05$; Figure 10.2) for foraging efficiency. The foraging efficiency (over all patches) of non-cued individuals was increased in the second block of trials compared to the first. This is due to an increase in foraging efficiency in the patches containing 10 and 15 food items per patch. In summary, foraging appears to become more efficient over time as a result of the monkeys concentrating their search effort on the densest patches.

Figure 10.2: Mean foraging efficiency at different prey densities for non-cued individuals (pooling species).



Now considering the number of searches performed by cued individuals, as was the case for non-cued individuals, there was no significant effect for trial block, so the number of searches (over all patches) did not differ in the second block of trials (6 - 10) compared to the first (1 - 5) ($F_{1, 38} = 1.984$, $p > 0.05$; Figure 10.3). However, there was a significant effect for prey density ($F_{3, 114} = 20.22$, $p < 0.05$) and a significant interaction between prey density and trial block ($F_{3, 114} = 15.94$, $p < 0.05$). So, as was also the case for the non-cued individuals, in the first block of five trials, searching appeared random across the four prey densities, but in the second block of five trials, searching appeared non-random, with a strong concentration of searching at the higher prey densities and a reduction in search effort on the patch containing no food items. In fact, three quarters of the monkey's search effort was concentrated upon the more profitable patches of 10 and 15 food items per patch, and only one quarter on the less profitable patches containing 0 and 5 food items per patch. There was also a clear, simple ranking or search effort in proportion to prey density in the different patches.

Figure 10.3: Mean number of searches at different prey densities for cued individuals (pooling species).



Now considering the effect this concentration of searching on the higher prey densities has for foraging efficiency, there was a significant effect for prey density ($F_{2, 76} = 3.91$, $p < 0.05$), a significant effect for trial block ($F_{1, 38} = 26.08$, $p < 0.05$) and a significant interaction between prey density and trial block ($F_{2, 76} = 4.16$, $p < 0.05$; Figure 10.4). So for both the first block and second block of trials, the foraging efficiency of cued individuals was greatest in the densest patches, and was (over all patches) greater in the second block than the first. Again, this increase was mainly due to an increase in foraging efficiency in the patches containing 10 and 15 food items per patch. So, as for the non-cued individuals, foraging becomes more efficient as a result of increasing search effort in the densest patches and reducing search effort on the patch containing no food items.

Figure 10.4: Mean foraging efficiency at different prey densities for cued individuals (pooling species).

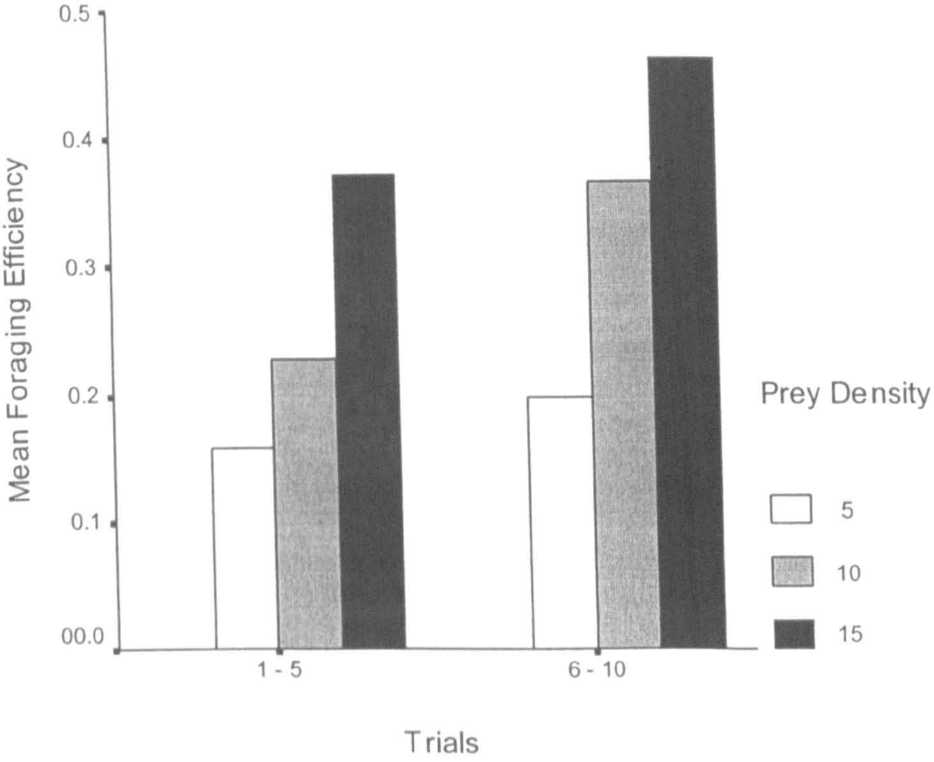


Figure 10.5 shows this increase in foraging efficiency (pooling prey density) over the ten trials for non-cued and cued individuals. A Repeated Measures ANOVA, pooling non-cued and cued individuals, revealed no significant effect for the presence or absence of cues on foraging efficiency ($F_{1,72} = 2.84$, $p > 0.05$; Table 10.3).

Figure 10.5: Mean foraging efficiency (pooling prey density) over trials 1 - 10 for non-cued and cued individuals (pooling species).

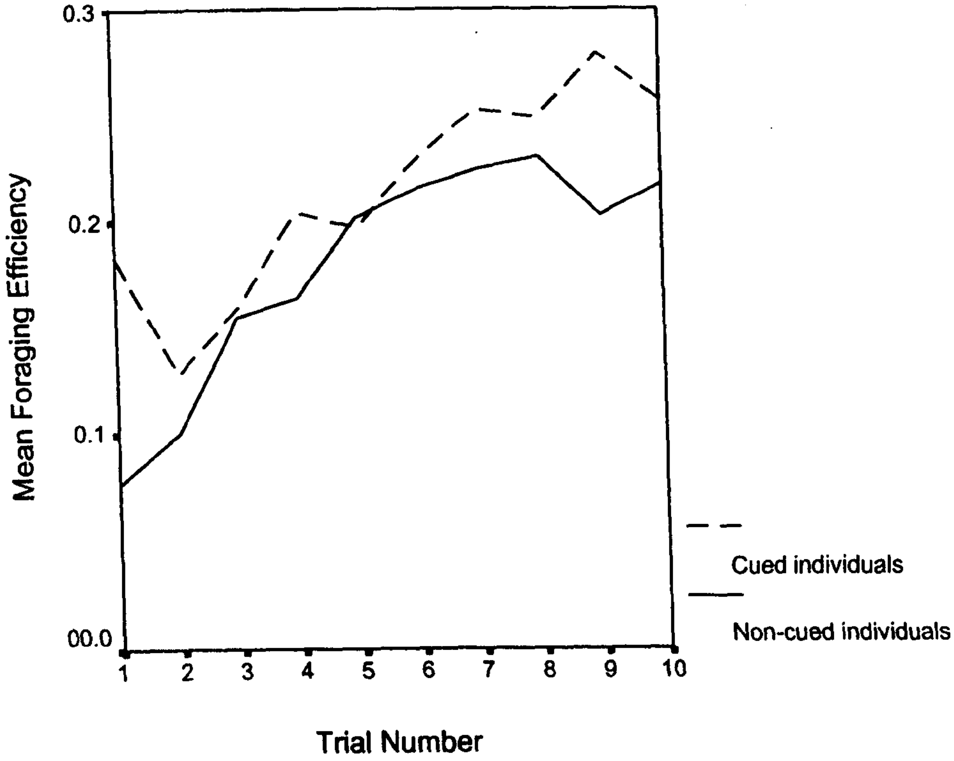


Table 10.3: Repeated Measures ANOVA F-values and mean scores for differences in the mean foraging efficiency by cued and non-cued individuals.

Prey Density	**n**	**Non-cued**		**Cued**	
		Mean	SD	Mean	SD
5	10	0.253	0.029	0.246	0.029
10	10	0.214	0.023	0.396	0.019
15	10	0.174	0.022	0.328	0.019

10.4 Discussion

The way that the food resources of tamarins are organised and become available in time and space is likely to be the major environmental constraint on their foraging success and to constitute an important selective pressure on efficiency in foraging behaviour. As species whose food is patchily distributed, information pertaining to the location, size and quality of food patches is likely to be significant. The results of this experiment suggest that captive tamarins have the ability to assess the relative densities of a single, sessile, hidden food type distributed in a series of discrete feeding patches and to use memory of relative patch quality to search selectively in the most profitable patches. Over a period of ten days, through sampling of all the available patches, they learned which patches were the most profitable and biased their searching towards them, increasing their foraging efficiency (number of successful searches per patch / number of searches per patch) in the process. This suggests that the tamarins are highly sensitive to small differences in foraging efficiency in the different patches resulting from small changes in the density of available prey within them. Mean (and individual) performance improved gradually suggesting incremental learning. Not only was sensitivity to the density distribution of prey evident in the distribution of their search effort, but also in their order of patch use. I noticed that, over time, they gradually began to initiate their daily foraging bouts in the richer patches first (10 and 15 food items per patch) and then moved to the lower density patches (0 and 5 food items per patch) towards the end of each trial. This could have been either a result of a decrease in hunger, so that they were willing to explore, or to a depletion of the food cases available for searching.

Captive *S. sciureus* have also been shown to readily discriminate between, and match their foraging effort (foraging time) to, the reward potential of different food patches (Andrews & Rosenblum, 1995). The authors suggest that this finding is consistent with a reinforcement matching perspective (where animals are thought to allocate behaviour among alternatives so as to match the reinforcement contingent upon those alternatives: see Commons *et al.*, 1982). Learning the distribution of resource patches in the environment and returning to the location of rich patches will be an adaptive foraging strategy for animals whose resources are temporally and spatially predictable/reliable. For such resources, the sample information obtained today from a given patch, can become the pre-harvest information used tomorrow prior to the exploitation of that patch.

We may conclude that, when foraging freely for patchily distributed food under naturalistic conditions, captive *S. fuscicollis* and *S. labiatus* forage largely by expectation of the relative energetic profitability of different food patches, at least when there is enough variation between these to allow them to develop clear expectations. By learning the location and quality (and hence profitability) of different feeding sites, and biasing their foraging towards the most profitable patches, the tamarins increased their foraging efficiency (and probably reduced the variance in their food intake). Wild tamarins have been shown to adopt a similar foraging strategy (to reduce variance in food intake) when foraging for nectar. Garber (1988a) found that during the dry season months of July and August at Río Blanco, Peru, when overall fruit production in the rain forest is low (Janson *et al.*, 1981), mixed-species troops of *S. fuscicollis* and *S. mystax* exploit the nectar rewards of *S. globulifera* through goal-directed travel and an ability to learn and remember the location of flowering *S. globulifera* trees in their home range. Although tree selection appeared to be based largely on minimising the distance travelled between feeding patches, in some cases, the proximity of the next nearest feeding tree of a given species, relative to the present feeding tree of that species, was not an accurate predictor of patch choice. Instead, trees characterised by higher mean feeding bout lengths were preferred over trees characterised by lower mean feeding bout lengths. If one assumes that feeding bout length bears some relationship to the amount of nectar available on a given tree, then variance in mean bout length is a measure of the consistency and relative quality of the tree. The tamarins passed over low quality feeding trees nearby in favour of high quality ones a further distance away. A preference for selecting the nearest and/or more productive target feeding trees thus characterises tamarin feeding patterns during food-limited periods of the year (i.e., dry season). This can be seen as evidence of a risk-sensitive foraging pattern, implying that the tamarins act so as to reduce the probability of short-term food or nutrient deficiencies by learning the location and renewal schedules of different feeding trees and concentrating their foraging on the most profitable trees.

In this study, although the tamarins came to initiate their foraging bouts in the most profitable patches, there was a tendency for the first move from the first patch to be to the next nearest patch, and only later was the next most profitable patch exploited. In a similar experiment with four baited food patches, *C. jacchus* were also found to favour exploiting patches adjacent to the one just exploited (MacDonald *et al.*, 1994). Selection of the next nearest feeding tree or patch is likely to be important for callitrichines in the energetically stressful food-limited dry season when, given their small size and high metabolic rates, travel costs are considerable. However, in this experiment, the monkeys can be assumed to not be energy-stressed and had only a short distance to travel between food patches so travel costs were negligible. Under such conditions, once having learnt the distribution of prey in the environment, the optimal foraging behaviour (that which maximises the rate of energy intake) in the short term is clearly to allocate *all* available searching effort to the patch (or patches) of greatest food density. This the monkeys did not do. Instead, they sampled all patches and persisted in sampling even the patch that did not contain any food items. This is important. Foraging is an inherently stochastic process (Oaten, 1977; Pyke, 1978; Maynard-Smith, 1978; Caraco, 1980; Stephens & Charnov, 1982). That is, foraging animals search for, encounter and handle their prey according to rules which are most accurately described by statements of probability (Oaten, 1977). Most parameters (such as the amount of energy obtained from an individual of a particular prey type) are random variables and take different values with different probabilities. As a result foraging animals can never be omniscient and uncertainty is likely to be a component of most foraging processes (Post, 1984). Such uncertainty is likely to be pronounced in highly patchy environments where there are substantial difficulties in 'monitoring' the availability of resources over a wide area. Given that, as described earlier, tamarins feed on often unpredictable, widely scattered and patchy foods (e.g., ripe fruits, insects), and given the constraints imposed on visibility in their densely vegetated habitat, uncertainty most probably characterises their foraging environments. One way in which tamarins might respond to this uncertainty (stochasticity) is to use a strategy to assessing patch quality and to continually update this information by sampling. The fact that the tamarins persisted in sampling the low quality patches may be taken as evidence of a long-term strategy for tracking temporal variability in the availability of patchily distributed food resources. As described earlier, although the short-term strategy for maximising energy intake is to forage only in the best patches, for animals such as tamarins whose food undergoes fluctuations in abundance over time, sampling all patches represents an adaptive long-term strategy to reduce variance in energy intake. In this regard, Pyke *et al.* (1977) write that

> "*in many situations the long-term and short-term optimal foraging strategies differ,... fitness is likely to be related most closely to the long-term outcome*" (p. 143).

In fact, it is likely that the optimal foraging strategy (with respect to long-term energy maximisation) will involve a balance between exploitation in the short-term and sampling to acquire information valuable in the long-term for improving future foraging success (Krebs *et al.*, 1978). It is conceivable that, for tamarins in the wild, there are times when food is abundant (e.g., during the wet season) and there is not continuous pressure on the monkeys to maximise their hunting efficiency. During such times energy may be used for maintenance activities but may also be used for exploratory foraging to gather information rather than food. For example, exploratory foraging may be important in allowing individuals to monitor changes in the spatial distribution and species composition of the food complex. The following experiment was designed to investigate how, given their tendency to sample the less-preferred patches, the tamarins respond to a change in the distribution of prey density amongst the different food patches (such that patches which had had a high density of prey now have a low density and vice-versa).

In the present experiment, the monkeys appeared to be able to learn the locations of the different patches with ease. Furthermore, the results for distribution of search effort and order of patch use according to differences in patch quality are consistent with the notion that these animals have an advanced spatial memory and develop spatially structured cognitive maps (Tolman, 1948, 1959)[1] of their surroundings and generate action with respect to these internal representations in order to increase their foraging efficiency. Tamarins have been shown elsewhere to possess and use spatial knowledge to solve foraging problems (e.g., Menzel & Juno, 1985, for *S. fuscicollis*; Garber & Dolins, 1996,

---

[1] The characteristics of cognitive maps were never well developed by Tolman. They can be considered as internal representations which simultaneously include information concerning the nature and relative positions of many particular objects within an individual's environment. One common implication of such representations is the prediction that animals possessing them ought to be capable of goal directed travel and to use the maps to minimise the distance travelled between successive objects visited and the frequency of path re-crossing. Tamarin troops show evidence of straight line, goal directed travel and the selection of nearest neighbour and/or productive feeding trees which may be indicative of an ability to compare the distance and direction from one feeding tree to many others in their habitat through the use of a cognitive map (Garber, 1988a, 1989; Garber & Hannon, 1993). Additional evidence for mental mapping is evident from the low incidence of backtracking and the ability to reach productive feeding trees by using a variety of different arboreal pathways.

for *S. mystax*; Garber, 1988a; Garber & Hannon, 1993, for mixed-species troops of *S. fuscicollis* and *S. mystax*; Dolins, 1993, for *S. oedipus*). However, despite tamarins being the focus of numerous field and laboratory investigations, still little is known regarding how they encode and use spatial information and perceptual cues during foraging. Given that the tamarins in this experiment chose to concentrate their searching on patches of high quality in order to increase their foraging efficiency, the following experiment investigated (in addition to their response to a change in prey density distribution) whether they use available local visual cues that reliably indicate high patch quality, or simply rely on spatial information, to locate these high quality patches following a change in their spatial location. There was no difference between cued and non-cued individuals in the speed of their specialisation on rich patches. In order to test whether individuals with the opportunity to use cues indicating patch quality do so, we need to switch the distribution of patch quality and compare the speed of response of cued individuals with that of non-cued individuals.

10.5 Experiment 9: Response to a Temporal Switch in the Distribution of Food Patch Quality

In Experiment 8, the prey densities in the different patches were held constant over time. The task required of the tamarins was to encode and associate spatial and patch quality (prey density) information that could be used to distinguish one patch from another, and then distinguish between the four patches. However, as described in the introduction to this chapter, the major natural foods of tamarins (ripe fruit and insects) exhibit complex patterns of distribution not only in space but also in time. We may therefore enquire how quickly tamarins respond to a temporal change in the distribution of prey density among the different patches from one stable configuration to another, or more specifically, how well the tamarins maintain their foraging efficiency when each single-species troop is rewarded at a low rate in the location that they had previously been rewarded at a high rate and vice versa. The hypothesis is that, given their tendency to sample all patches, individual tamarins will eventually recover to near their original performance by switching their greatest search effort back to the most dense patch.

Moreover, as in Experiment 8, for half the pairs the richest patches were visually cued with red ribbons, and for the other half they were not. Therefore, for half the pairs the switch in prey density was visually cued and for the other half it was not. Consequently, comparing the foraging behaviour of cued and non-cued individuals enabled me to determine whether the cued individuals used the cues in their foraging or not and hence the relative importance of spatial memory and visual cue associative learning in responding to temporal changes in food density. In their natural habitat, the food of tamarins can occur in spatial association with topographical features (e.g., within particular vegetation densities or plant communities, or at particular heights). This type of distal information is likely to aid in remembering the location of particular food patches. In addition, some food types may be more closely associated with local visual cues (e.g., signs of insect damage indicating the presence of insects) which can be used reliably to increase the likelihood of encounter with these food types.

There is reason to suspect that the divergent foraging styles of *S. fuscicollis* and the *S. mystax* group (see Section 1.2.4) may mean that *S. fuscicollis* and *S. labiatus* differ in their ability or propensity to associate local visual cues with the presence of hidden food at feeding sites. For example, Terborgh (1983) found that seasonal variation in the insect capture rate (number of successful searches per unit time) of the leaf gleaning *S. imperator* correlated more strongly with variation in search rate (number of searches per unit time) than with success rate (proportion of searches which were successful). This was interpreted to mean that *S. imperator* does not conduct insect searches at random but in response to some perceived sign of insect activity or presence (e.g., rolled leaves, damaged foliage etc.) since, if an animal were visually scanning its environment for signs of prey and responding only to such signs in initiating searches, a change in prey abundance would translate directly into a change in the frequency of telltale signs and hence into a change in search rate. The opposite was found for *S. fuscicollis*. In this species, variation in capture rates was better explained by variation in success rates. This was interpreted to mean that *S. fuscicollis* are blind foragers since, if an animal were foraging blindly (i.e., searching leaves or other substrates purely at random) a change in prey abundance would translate directly into a change in success rate. According to the evidence provided by Terborgh then, given that *S. labiatus* insect forages in manner very similar to *S. imperator* (Garber, 1993a), one would expect *S. labiatus* to be better able than *S. fuscicollis* to associate local visual cues with the presence of an abundance of insect prey (patch quality).

The aims of the experiment were to investigate the effect of a temporal change in food patch quality (prey density) on feeding efficiency; and to investigate the extent and manner in which each species uses spatial memory and associative visual cues in responding to such a change.

10.5.1 Study Animals

The study animals were those tested in Experiment 8 (see Section 10.2.1). The female *S. labiatus* from SL6 was in the late stages of pregnancy during testing.

10.5.2 Design

The day after each pair had completed the ten test trials of Experiment 8, they were released onto the density distribution opposite to that that they had experienced in Experiment 8 (e.g., if they experienced A15, B5, C10, D0 in Experiment 8, then in Experiment 9 they were presented with A0, B10, C5, D15: see Table 10.1). Note that the total number of food items (over all patches) remained the same as that in Experiment 8. This new distribution was held constant for ten daily test trials (in order that comparisons could be made in Experiment 10 between naïve individuals foraging with a naïve conspecific and naïve individuals foraging with a knowledgeable congener, both sets of naïve individuals having had experience of a particular distribution for ten trails). For SF7 and SL7, and SF9 and SL9, the experiment was carried out as described above, except that the switch in patch quantity was cued, such that the patches now containing 15 and 10 items were marked by the presence of five red ribbons in each patch (as they were for these pairs in Experiment 8: see Table 10.1).

10.5.3 Procedure

Habituation and training were not required. Test trials were conducted as in Experiment 8 (see Section 10.2.3).

10.5.4 Recording Methods

Recording methods were exactly as in Experiment 8 (see 10.2.4).

10.5.5 Data Analysis

Data analysis was as in Experiment 8 (see 10.2.5). The data were split into two blocks (the first five trials and the second five trials after the switch). Comparisons are made between the five immediately before the switch (trials 6 - 10 from Experiment 8) and the five immediately after the switch (trials 11 - 15 from this Experiment). Non-cued and cued individuals were analysed separately for differences in foraging efficiency and the number of searches for trial block and for prey density using the Repeated Measures ANOVA. I hypothesised that foraging efficiency would decrease following the switch in patch quality for both non-cued individuals and cued individuals, but that they would recover rapidly. Furthermore, the cued individuals should recover more rapidly than the non-cued individuals if they were using the cues. Significance was set at alpha < 0.05. Competitive behaviours were so few as to not warrant analysis.

10.6 Results

Results are presented for the non-cued and cued individuals separately. A Repeated Measures ANOVA, pooling species, revealed no main effect for species for either the number of searches or foraging efficiency for non-cued and cued individuals (Table 10.4), Consequently, the results presented below are for the data set pooled for species.

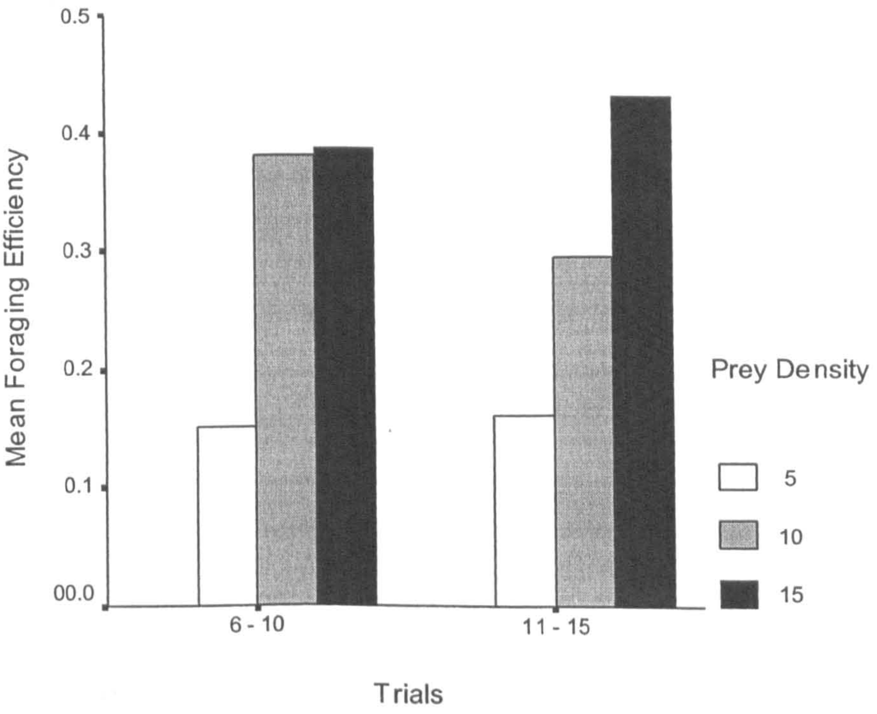
Table 10.4: Repeated Measures ANOVA F-values and mean scores for species differences in the mean number of searches and mean foraging efficiency by cued and non-cued individuals.

Individuals	**Variable**	**Species (*S. fuscicollis* / *S. labiatus*)**
Cued	Number of searches	$F_{1,37} = 1.56,\ p > 0.05$ (8.57, 7.88)
	Foraging efficiency	$F_{1,37} = 1.34,\ p > 0.05$ (0.30, 0.27)
Non-cued	Number of searches	$F_{1,38} = 4.04,\ p > 0.05$ (8.32, 7.40)
	Foraging efficiency	$F_{1,33} = 3.74,\ p > 0.05$ (0.31, 0.26)

Non-cued Individuals

Considering the foraging efficiency of non-cued individuals first, there was no significant effect for trial block ($F_{1, 34} = 2.88$, $p > 0.05$), so foraging efficiency was not decreased in the second block of trials (after the switch) compared to the first (before the switch). There was a significant effect for prey density ($F_{2, 68} = 4.34$, $p < 0.05$) but no significant interaction between prey density and trial block ($F_{2, 68} = 1.90$, $p > 0.05$; Figure 10.6). So foraging efficiency was greatest in the densest patches in the five trials both before and after the switch. Non-cued individuals appeared, then, to recover rapidly from the switch in prey density in the different patches, responding to the new density distribution within five trials of the switch such that foraging efficiency (over all patches) was not significantly reduced. There was no difference in the mean number of searches (over all patches) performed in the second block of trials compared to the first ($F_{1,39} = 0.00$, $p > 0.05$ (7.89, 7.92)).

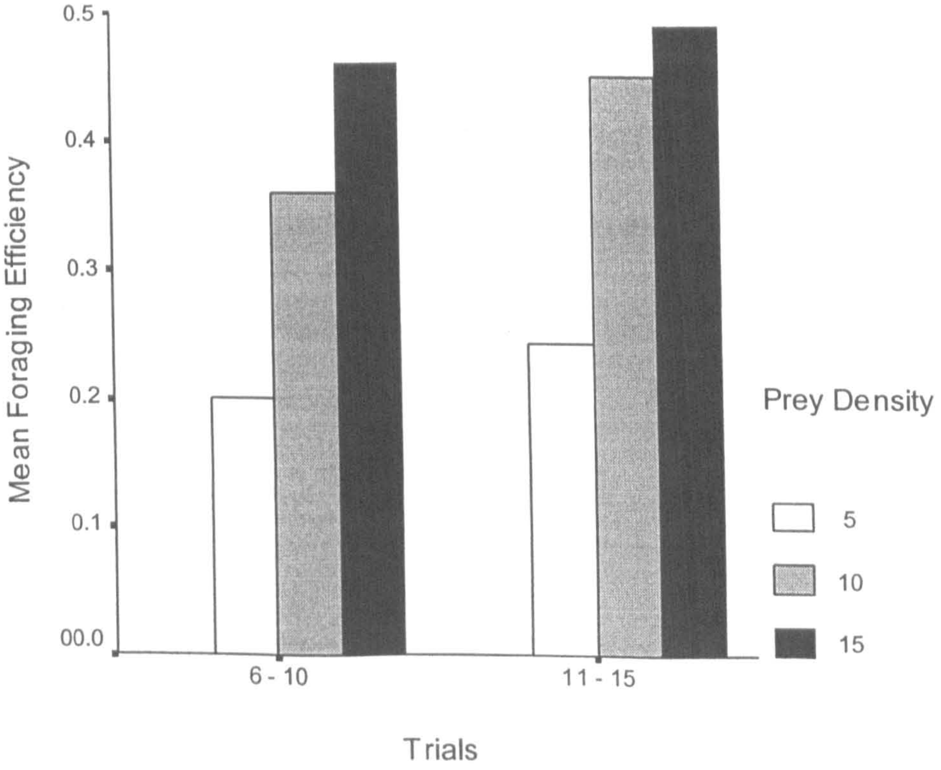
Figure 10.6: Mean foraging efficiency at different prey densities for non-cued individuals (pooling species).



<u>*Cued Individuals*</u>

Now considering the foraging efficiency of cued individuals, there was a significant effect for trial block ($F_{1, 38} = 26.08$, $p < 0.05$). Foraging efficiency was actually increased in the five trials following the switch compared to the five before. There was also a significant effect for prey density ($F_{2, 76} = 3.91$, $p < 0.05$) but no significant interaction between prey density and trial block ($F_{2, 76} = 4.16$, $p < 0.05$; Figure 10.7). So foraging efficiency was greatest in the densest patches both before and after the switch. There was no significant difference in the mean number of searches (over all patches) performed in the second block of trials compared to the first ($F_{1,39} = 1.33$, $p > 0.05$ (7.84, 8.62)).

Figure 10.7: Mean foraging efficiency at different prey densities for cued individuals (pooling species).



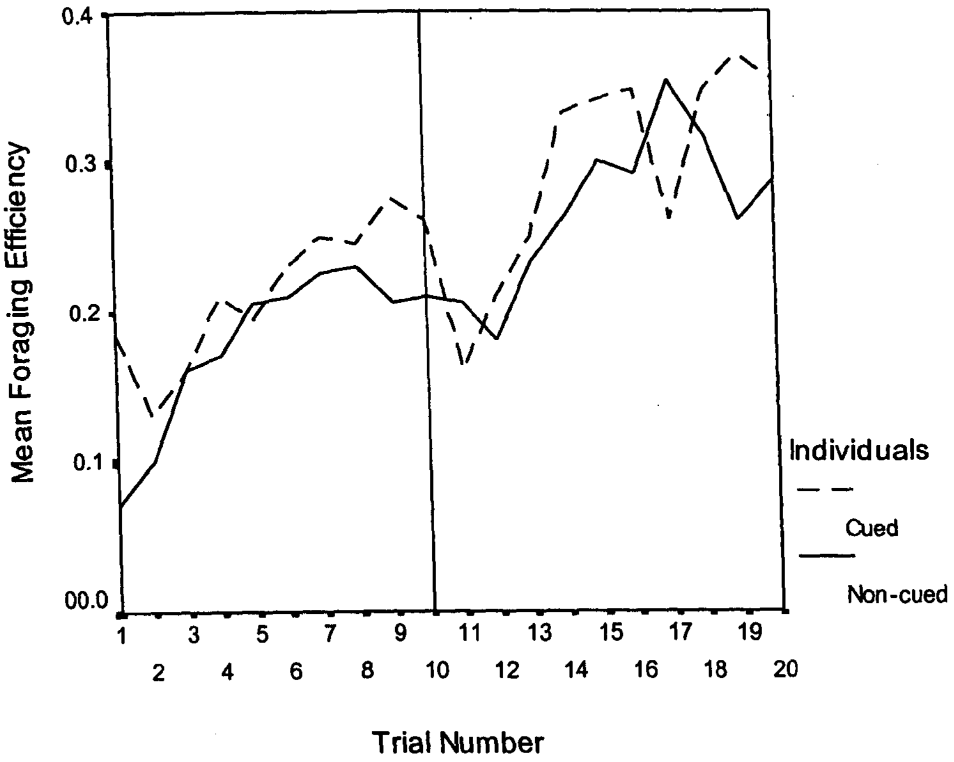
So again, as for the non-cued individuals, the cued individuals appear to rapidly adjust to the switch in prey density in the different patches, responding to the new density distribution within five trials. Furthermore, unlike the non-cued individuals, the cued-individuals managed to increase their (overall) foraging efficiency after the switch (a consequence of an increase in foraging efficiency in all three patches containing food). Furthermore, this increase was not a consequence of an increase in search effort. However, a Repeated Measures ANOVA, considering trials 11 - 15 only (the five after the switch), and pooling cued and non-cued individuals, revealed no significant effect for the presence or absence of cues on foraging efficiency ($F_{1,79} = 0.95$, $p > 0.05$; Table 10.5).

Table 10.5: Repeated Measures ANOVA F-values and mean scores for differences in the mean foraging efficiency by non-cued and cued individuals in trials 11-15.

Prey Density	**n**	**Non-cued**		**Cued**	
		Mean	SD	Mean	SD
5	5	0.221	0.032	0.223	0.032
10	5	0.273	0.038	0.200	0.039
15	5	0.268	0.034	0.248	0.034

In summary, both cued and non-cued individuals appeared able to recover their foraging efficiency to pre-switch levels within five trials after the switch and after only a temporary drop in foraging efficiency (Figure 10.8).

Figure 10.8: Mean foraging efficiency (pooling prey density) over trials 1 - 20 for non-cued and cued individuals (pooling species).



10.7 Discussion

Experiment 9 showed that, in an otherwise stable environment, the tamarins could readily detect and respond to a simple temporal change in the distribution of prey density amongst food patches with only a temporary drop in foraging efficiency. Within five trials of the switch in prey density distribution, the monkeys had learned the new location of the patches with the greatest prey density (one of which had previously been without prey) and had begun to use this information to forage efficiently. In a field experiment on Padre Isla, Peru, Garber and Dolins (1996) found that wild *S. mystax* are able to re-learn the new locations of baited feeding patches following a similar switch within two days.

The results of this experiment are again consistent with the notion that these animals have an advanced spatial memory and develop spatially structured cognitive maps of their surroundings and generate action with respect to these internal representations to increase their foraging efficiency. Evidence of advanced spatial memory in tamarins has been reported elsewhere (Menzel & Menzel, 1979; Menzel & Juno, 1982, 1984, 1985; Garber, 1988a; Dolins, 1993; Garber & Hannon, 1993; Garber & Dolins, 1996) and has likely evolved as an adaptation for them to exploit efficiently their small, patchy and widely scattered, piecemeal but often asynchronously ripening (within and between species) fruit resources in the densely vegetated, and hence visually limiting, rain forest (Garber, 1989). However, despite evidence for an advanced spatial memory, little is certain regards how this spatial memory is organised. This is a reflection of the difficulties in controlling relevant variables, particularly in the field, sufficiently to allow firm conclusions about the mechanisms guiding spatial movements in animals.

The non-cued individuals improved their foraging efficiency before the switch (Experiment 8) and after the switch (this experiment) by learning and returning to the new location of the richest patches without the aid of the local visual cues (red ribbons) provided to the cued individuals. The fact that their speed of response to the switch did not differ from that of the cued individuals implies that the cued individuals did not use the local visual cues as indicators of patch quality. Instead, they too appeared to rely on recall of a learnt association between patch quality and spatial location (spatial memory). More compelling evidence for a reliance upon spatial memory is that none of the cued individuals went directly to the new richest patches (10 and 15 prey items per patch), on commencement of the trials immediately following the switch (the new location of these being cued by the red ribbons). Instead, both cued and non-cued individuals went directly to the previous location of the richest patches. This is further evidence for expectations regarding the amount of food available within a patch having a significant influence on foraging decisions and furthermore, in conjunction with the specialisation observed in Experiment 8, indicates that the monkeys are following a 'win-stay, lose-shift' searching strategy (Levine, 1959) with respect to the richest patches (i.e., returning to the location of a previously successful foraging bout, as opposed to shifting to an alternative area, and avoiding locations that were previously unsuccessful: see Olton, 1982). A tendency to win-stay without special training and without reinforcement has also been found by Menzel and Juno (1985) for *S. fuscicollis*, and by MacDonald *et al.* (1994) for *C. jacchus*. The decision for an animal to stay or shift (i.e., the optimal foraging strategy) depends on the way in which its food resources are distributed in space and time. Individuals who adopt a search strategy appropriate to the distribution of food in the environment should have an adaptive advantage over individuals who adopt an inappropriate strategy. Re-inspection of exact locations that previously contained food can be expected to improve an animal's chances of foraging efficiency for resources that are not depleted in just one visit or that renew over an extended period of time (e.g., ripening fruits or ants emerging from a nest). Menzel and Juno (1985) suggest that their results for *S. fuscicollis* are consistent with field data on the foraging habits of *S. fuscicollis* in the wild in relation to their major fruit resources which ripen piecemeal (Terborgh, 1983). This pattern of fruit ripening implies that only a very small amount of food is available for eating at any given locus at any one time, but also that a reliable (though scant) supply can be obtained at the same loci over a period of many weeks. Thus a win-stay search strategy would be more adaptive than a win-shift strategy in this context. To the extent that food searching strategies become a species typical characteristic, species that search for reliable food resources ought to exhibit a win-stay strategy in the laboratory. Menzel and Juno (1985) suggest also that, although it initially goes against their grain, tamarins can also learn to 'win-shift, lose-return' (Levine, 1959).

Such a strategy would be adaptive when foraging for self-renewing but slowly ripening resources such as nectar. The results of Garber's (1989) field study suggest that *S. fuscicollis* and *S. mystax* use a win-shift strategy to avoid locations that previously contained food when feeding upon fruit and exudates, in as much as, after the monkeys had visited a tree they were unlikely to return to it for at least two days. A 'win-shift' strategy is also likely to be a common element of a species' foraging pattern in the context of exploration and resource sampling in order to update information on the future availability of food within food patches. We saw in Experiment 8 that variability in their foraging environment can cause tamarins to win-shift to gather information rather than food (sampling). In fact, an ability to switch between these search strategies (behavioural flexibility) is likely to be adaptive for these monkeys. If resource renewal is rapid relative to depletion, then they should return to recently depleted patches. If renewal is slow, then the optimal strategy is to avoid recently depleted patches.

Returning to the use of cues during foraging, although it has been suggested that wild tamarins may use local visual cues to locate the presence of insect prey (Terborgh, 1983), in this experiment, comparing the results from pairs for which local visual cues (indicating a large amount of insect prey) were present with those for which they were not, since there were no species differences, it appears that neither *S. fuscicollis* nor *S. labiatus* individuals with the opportunity to use the cues did so [1]. The same result has been found

---

[1] It would have been theoretically possible to perform multiple regression, using the very same variables Terborgh (1983) used to investigate whether *S. fuscicollis* and *S. imperator* initiate searches in response to signs of prey, to determine whether the cued *S. fuscicollis* and *S. labiatus* used the cues in their foraging or foraged blindly (see 10.5). However, this analysis was not done because of the problems inherent in addressing which of the independent variables in a multiple regression equation is the most important in accounting for variability in the dependent variable and because of problems with independence of the data.

with wild *S. mystax*. During the course of a six day study in which red flags were used to indicate baited food platforms, *S. mystax* did not select rewarded platforms at a greater rate than expected by chance (Garber & Dolins, 1996). These findings (for tamarins) are in contrast to what has been found regards cue association/the use of cues during foraging in similar experiments with *Cebus capucinus* (white-faced capuchin) (Garber & Paciulli, 1997), *M. mulatta* (Drea & Wallen, 1995) and *Papio papio* (Guinea baboon) (Lepoivre & Pallaud, 1985, 1986). These species were found to differentiate baited from unbaited food patches on the basis of an associated colour cue. Garber and Paciulli (1997) suggest that for *C. capucinus* the use of visual cues as indicators of the presence of food is an adaptive response to their insect prey which spend the day concealed from view within dead or curled leaves, or embedded in knotholes in bark, palm fronds and the base of bromeliads, and require the capuchins to actively manipulate and search inside these closed micro-habitats (extractive foraging). By paying attention to signs of insect presence (e.g., damaged leaves or subtle differences in the colour and texture of holes in tree branches and trunks) these monkeys can increase the likelihood of encounter with insect prey.

Garber and Paciulli, referring to the study by Garber and Dolins (1996), further suggest that, since *S. mystax* rarely exploit concealed or embedded insect prey but instead take insects that spend the day exposed to view, resting on top of green foliage, it is possible that they rely primarily upon visual sighting of foods and distant landmarks, rather than on local landmarks in locating food patches and initiating searches for food. Since *S. labiatus* also rarely exploit concealed or embedded prey, they too may also rely on direct visual sighting of insect prey rather than on indicators of their presence in initiating insect searches. This is a possible explanation for their failure to use the cues in this experiment. The prey of *S. fuscicollis* do spend the day concealed from view within forest debris and embedded in bark. According to Garber and Paciulli's reasoning for *C. capucinus*, one would expect *S. fuscicollis* to rely on local visual cues to increase the likelihood of encountering this concealed or embedded prey. However, Terborgh (1983) suggests that *S. fuscicollis* is blind to such cues (See Section 10.5). The fact that *S. fuscicollis* did not use the visual cues indicating the presence of an abundance of insect prey in this experiment would seem to support Terborgh's argument.

Although both species did not appear to use the cues, it is difficult to draw conclusions from the data as to whether this was because they were unable to perceive the cues; because they were able to perceive the cues but were unable to learn the association between these and patch quality; because they were able to learn the association but for some reason failed to do so (e.g., because the spatial contiguity between the cues and the food was not great enough: Jarvik, 1953); because one patch without cues still had five prey items in it; or because the rich patches became depleted quite quickly, yet the cues remained present (this may have been a particular problem for secondary attendants arriving in the patch after it had been depleted by the primary attendant); or because they learnt the association between the cues and patch quality but did not use them in favour of a reliance upon spatial location information.

It is possible that the monkeys were unable to perceive the red ribbons against the green foliage of the 'Free-Range Area' due to their colour vision. As described in Section 1.2.9, New World monkeys show great inter-species and intra-species variation in their colour vision. Within a population of New World primate species, there are typically six different types of colour vision genotypes possible: the males may be one of three kinds of dichromat (i.e., all males are "colour blind") while females may be one of three types of dichromat or three types of trichromat. Trichromacy is thought to be advantageous in the detection and identification of food, particularly yellow and orange ripe fruits in the dappled light of leaves (Polyak, 1957; Mollon 1989, 1991; Osorio & Vorobyev, 1996; Regan *et al.*, 1996). Thus, in retrospect, perhaps it would have been better to use cues not based upon colour, but upon pattern (since in Experiment 5, *S. labiatus*, at least, appeared to show evidence of a learnt association between pattern and food quantity) or more ecologically valid stimuli such as perforated leaves (natural indicators of insect damage and thus presence). In fact, I have obtained evidence since conducting this study that dichromatic *S. fuscicollis* and *S. labiatus* individuals are indeed at a disadvantage in the detection and selection of orange and red items (coloured fruits) (Buchanan-Smith *et al.*, unpubl. MS). Even if the cues are perceivable to the monkeys, they are unlikely to be perceived in the same way due to colour vision polymorphism. Obviously further research is needed regards how this polymorphism affects behaviour in relation to feeding.

10.8 Experiment 10: Divergent Knowledge About Food Patch Quality

As described in the introduction to this chapter, within their home territory, tamarins can achieve maximum foraging success as a direct result of intimate knowledge of the locations of their resource patches, the productivity (quality) of these, and the schedule on which each has last been harvested. As social foragers, and given that, as we have seen in earlier chapters, associating species in tamarin mixed-species troops are capable of learning from one another about the presence and location of food, food palatability, and method of access, one might also expect individual tamarins to attend to the behaviour of their conspecific and congeneric troop-mates and to take advantage of their patch quality assessments by noting their foraging success in different patches. In theory, knowing that other troop members (of either species) are doing well in a patch may enable individuals to generate estimates of patch quality more rapidly and accurately than they could do alone and thereby forage more efficiently (Clark & Mangel, 1986). In this way, social learning may allow them to track environmental variability more efficiently than would asocial learning alone, as social learners can quickly and safely home in on appropriate behaviour by sharing up to date foraging information (Laland *et al.*, 1996). Mixed-species troop formation, by increasing troop size, would increase the opportunity for transfer of this information accordingly. The advantage from social learning of patch quality need not be precluded by the vertical segregation between associating species provided both are able to feed in the feeding patches discovered by their congeners in separate strata. Leading individuals of either species may encounter clusters of feeding trees within their habitual strata and, through their subsequent foraging behaviour, may act as 'indicators' of high or low quality feeding patches within these.

The aim of the experiment was to investigate whether, when given incorrect knowledge concerning patch quality, naive individuals capitalise upon the correct knowledge of a congener to increase foraging efficiency.

10.8.1 Study Animals

The study animals were two adult male-female pairs of *S. fuscicollis* (SF3, SF6: Table 4.1) and *S. labiatus* (SL3, SL6: Table 4.2) from Experiments 8 and 9. A son and daughter were born to SL6 during testing. Normally maintained as mixed-species troops (SF3 & SL3; SF6 & SL6), the single-species pairs within the mixed-species troops were separated and re-mixed with their congeneric pair to from mixed-species pairs when necessary according to experimental protocol.

10.8.2 Design

The experimental design required the creation of pairs of individuals possessing divergent knowledge (correct and incorrect) concerning the distribution of prey density across the different patches. Thus the male and female from each of the non-cued single-species pairs (tested in the first summer of data collection) were separated and mixed with a familiar congeneric male-female pair to form mixed-species pairs consisting of a male of one species and a female of the other each having had experience of contrasting (opposite) distributions [1]. These individuals did not have experience of the cues used in Experiments 8 and 9 and no cues were present during this experiment. Each mixed-species pair was released onto one of the contrasting distributions from Experiment 9 and allowed to forage freely in five consecutive daily test trials (21 - 25). The experiment was counterbalanced for sex, species and distribution of prey density (see Table 10.6).

Comparisons are made between naïve individuals learning a new distribution along with a naïve conspecific pair-mate (trials 11 - 15 from Experiment 9, immediately after the switch) and those *same* naïve individuals learning a new distribution along with a knowledgeable congener (trials 21 - 25: this experiment). Since, initially during trials 11 - 15 and trials 21 - 25, prior information about the distribution of resources in the environment is *incorrect* for what I have termed naïve individuals, they must rely upon

---

[1] Unfortunately, due to the troops available for testing and due to the tendency of tamarins to react aggressively to unfamiliar, unrelated conspecifics, I was unable to make the appropriate comparisons between a male and female of the same species with experience of contrasting distributions in order to negate this species confound.

Table 10.6: Distribution of prey density in patches A, B, C and D, for male-female mixed-species pairs tested in Experiment 10.

	SF3 male	**SL3 female**	**SF3 female**	**SL3 male**	**SF6 female**	**SL6 male**	**SF6 male**	**SL6 female**
Experiment 9 (trials 11-20)	15, 5, 10, 0	0, 10, 5, 15	15, 5, 10, 0	0, 10, 5, 15	0, 10, 5, 15	15, 5, 10, 0	0, 10, 5, 15	15, 5, 10, 0
	↓	↓	↓	↓	↓	↓	↓	↓
Experiment 10 (trials 21-25)	15, 5, 10, 0	15, 5, 10, 0	0, 10, 5, 15	0, 10, 5, 15	0, 10, 5, 15	0, 10, 5, 15	15, 5, 10, 0	15, 5, 10, 0
Correct knowledge?	yes	no	no	yes	yes	no	no	yes

sampling information accumulated during patch use (e.g., the time spent in the patch, the number of food items obtained, and the time since the last food capture) in order to increase their foraging efficiency. However, they do *also* have access to ‘public information’ (Valone & Giraldeau, 1993), acquired by noting the foraging success of other troop members in the same patch. In trials 11 - 15, this public information is the incorrect information of a naïve conspecific pair-mate; in trials 21 - 25, it is the correct information of a knowledgeable congeneric troop-mate; so any differences in performance between these two blocks of trials might be attributable to this divergence in available knowledge/information.

By observing the behaviour of their knowledgeable congener, for example, which patch it goes to first, its sequence of patch use, and its subsequent foraging behaviour in those patches (since there is spatial contiguity in that food items are consumed within the food patches and not taken elsewhere for consumption), naïve individuals may learn the location of the most profitable feeding areas more quickly than when foraging with a naïve conspecific. The question then being: given this divergent knowledge concerning patch quality, do species attend to the behaviour of their knowledgeable congeners in order to increase foraging efficiency? The experiment began the day after Experiment 9 and was conducted between July and September, 1996.

10.8.3 Procedure

Habituation and training were not required. Test trials were conducted as in Experiment 8 (see Section 10.2.3), except that the monkeys received a total of only five test trials and no cues were present. Individuals were tested in mixed-species pairs but were re-united with their conspecific pair-mate immediately after testing until the following test trial.

10.8.4 Recording Methods

Recording methods were exactly as in Experiment 8 (see Section 10.2.4).

10.8.5 Data Analysis

Given the small sample size (just four naïve individuals foraging with four knowledgeable congeners), it was deemed best to present data for each naïve individual separately. The Paired-Samples T test was used to compare the number of searches and foraging efficiency of naïve individuals learning a new distribution along with their naïve conspecific pair-mates (trials 11 - 15 from Experiment 9) and those same naïve individuals learning a new distribution along with their knowledgeable congeneric troop-mates (trials 21 - 25 from this experiment). Significance was set at alpha < 0.05. In addition, from the data on individual patch entry and exit, it was possible to calculate the number of times naïve individuals followed their knowledgeable congener into a patch and vice-versa [1]. These were compared with the Binomial Test with the test proportion set at 0.5. Data on the direction and total frequency of competitive interactions and on food calls are also presented.

---

[1] I assumed that the individual that first entered a rich food patch and initiated a feeding bout there had encountered the patch via its own cognitive ability and experience of the initial density distribution of the food patches. The same cannot be assumed for secondary visitors because the monkeys followed one another into food patches, and the rich patches were often vocally advertised, whether or not deliberately, by their initial attendants. Secondary attendants may thus have relied upon the less profitable strategy of basing their foraging decisions on the foraging behaviour of the primary attendant who discovered and exploited the food first.

10.9 Results

For the naïve *S. fuscicollis* male, foraging efficiency was significantly reduced in the presence of a knowledgeable congener compared to performance when with a naïve conspecific (Table 10.7). There was a non-significant trend for reduced foraging efficiency when with a knowledgeable congener for the *S. fuscicollis* female and *S. labiatus* male also. No difference was found for these individuals in the number of searches when foraging with a knowledgeable congener compared with a naïve conspecific. The *S. labiatus* female, increased her foraging efficiency when foraging in the presence of a knowledgeable congener compared to when with a naïve conspecific. However, this may simply have been a consequence of an increase in the number of searches performed [1].

Table 10.7: Paired-Samples T test values and mean scores for differences in mean foraging efficiency and mean number of searches by naïve individuals when foraging with a naïve conspecific (trials 11 - 15) compared to when foraging with a knowledgeable congener (trials 21 - 25).

Variable	**Species**	**Sex**	**Trial Block (11 - 15, 21 - 25)**
Foraging efficiency	*S. fuscicollis*	Male	t = 3.01, *df* = 14, **p < 0.05** (0.298, 0.082)
		Female	t = 1.56, *df* = 14, p > 0.05 (0.367, 0.253)
	S. labiatus	Male	t = 1.89, *df* = 14, p > 0.05 (0.271, 0.127)
		Female	t = -5.19, *df* = 14, **p < 0.05** (0.142, 0.409)
Number of searches	*S. fuscicollis*	Male	t = 1.34, *df* = 19, p > 0.05 (9.75, 9.00)
		Female	t = 0.41, *df* = 19, p > 0.05 (7.70, 5.55)
	S. labiatus	Male	t = 0.68, *df* = 19, p > 0.05 (6.90, 6.80)
		Female	t = - 2.13, *df* = 19, **p < 0.05** (7.00, 9.30)

Bold indicates a significant result.

---

[1] This female was lactating during trails 21 -25 and, free from the burden of carrying her twin offspring, may have been attempting to increase her energy intake through an increase in overall search effort.

Thus it would appear that, in general, the foraging efficiency of naïve individuals is not increased as a result of foraging with a congener knowledgeable about patch quality. To examine this situation in detail, we need to look at the proportion of prey items taken by each individual in each pair in each trial (Figures 10.9 to 10.12). Each of the four figures relates to one of the four naïve individuals foraging with a naïve conspecific (trials 11 - 15) and with a knowledgeable congener (trials 21 - 25).

Figure 10.9: Percentage of prey taken in each trial by the naïve *S. fuscicollis* male when with a naïve conspecific (trials 11 - 15) and when with a knowledgeable congener (trials 21 - 25).

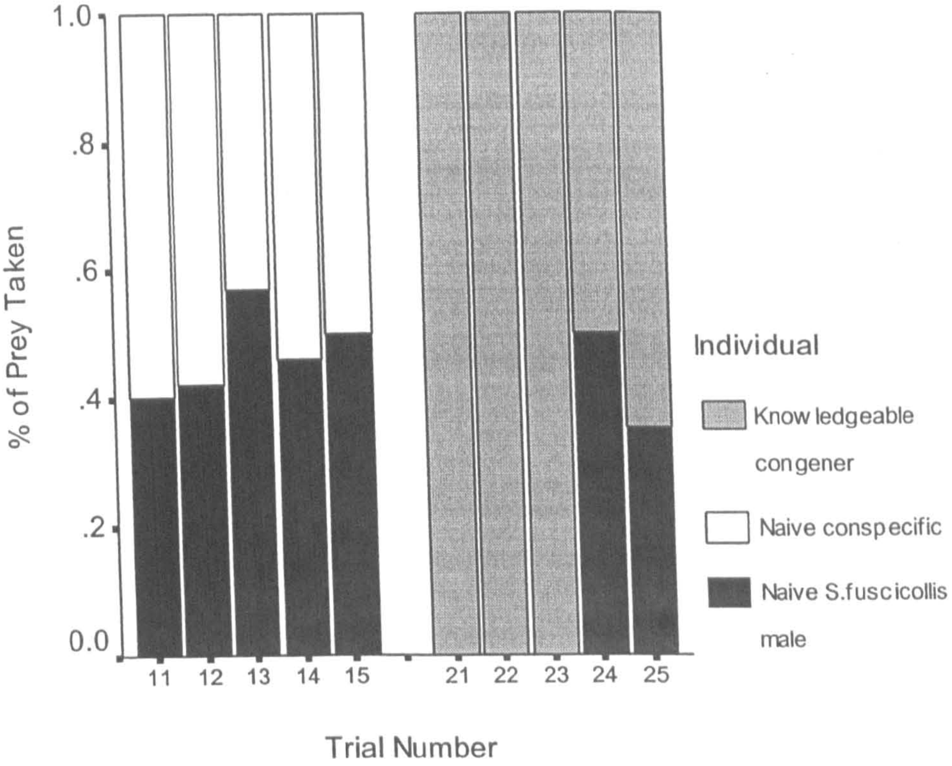


Figure 10.10: Percentage of prey taken in each trial by the naïve *S. fuscicollis* female when with a naïve conspecific (trials 11 - 15) and when with a knowledgeable congener (trials 21 - 25).

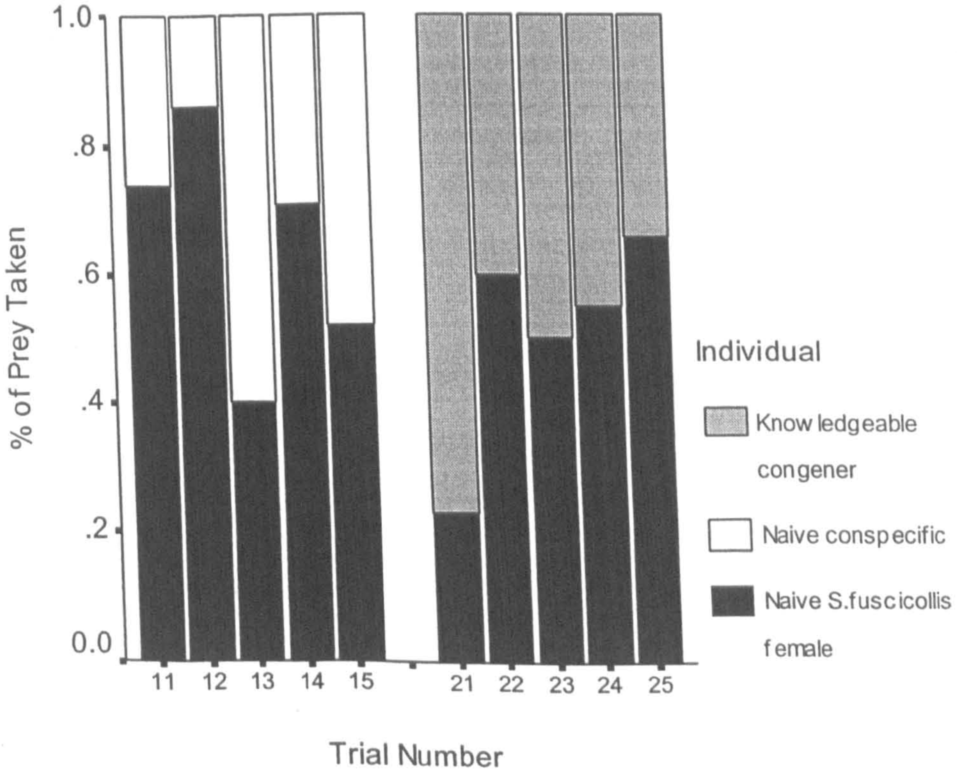


Figure 10.11: Percentage of prey taken in each trial by the naïve *S. labiatus* male when with a naïve conspecific (trials 11 - 15) and when with a knowledgeable congener (trials 21 - 25).

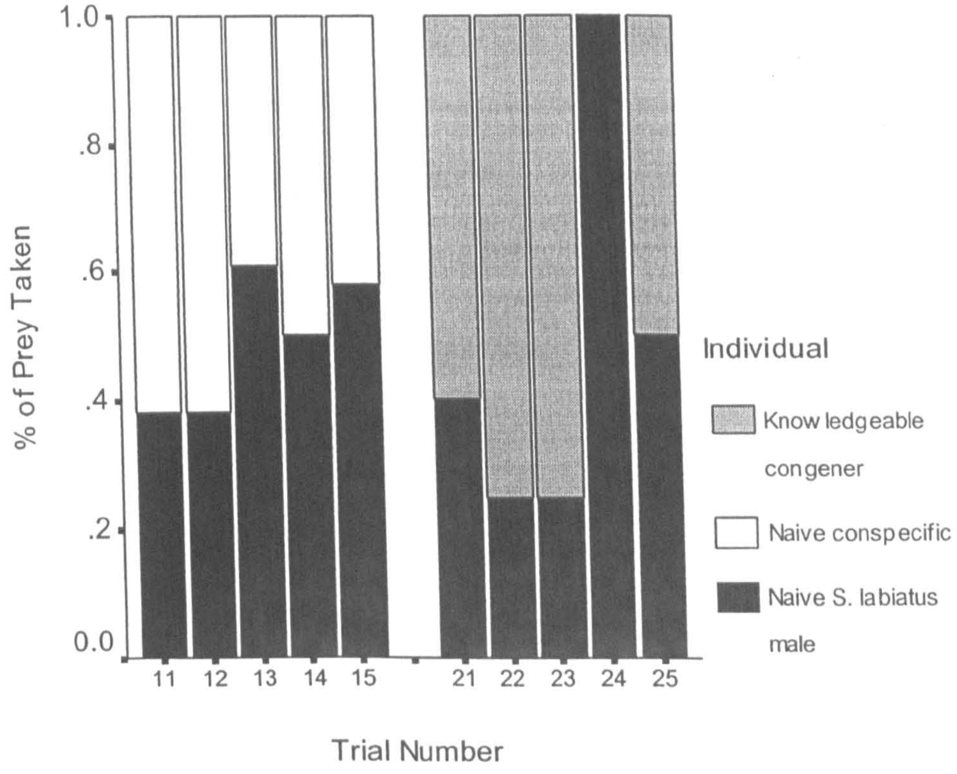
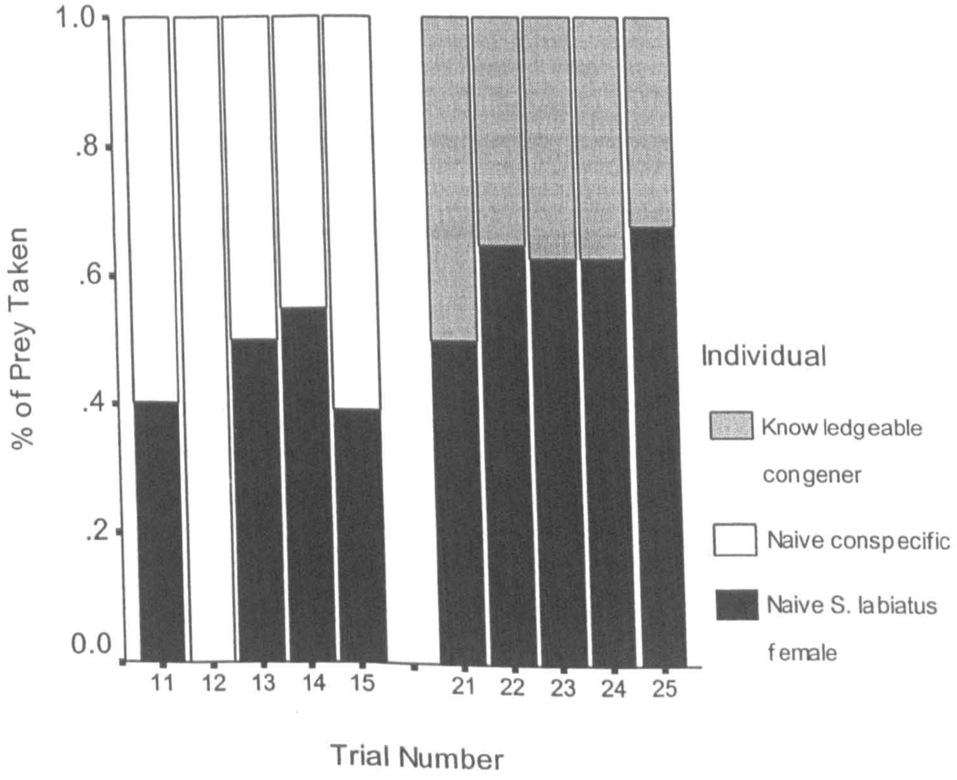


Figure 10.12: Percentage of prey taken in each trial by the naïve *S. labiatus* female when with a naïve conspecific (trials 11 - 15) and when with a knowledgeable congener (trials 21 - 25).



So the presence of a knowledgeable congener does not appear to increase foraging efficiency for the *S. fuscicollis* male and female and *S. labiatus* male (they obtained a smaller proportion of the food items available than they did when foraging with a naïve conspecific). The *S. labiatus* female, however, was able to increase her foraging efficiency, obtaining proportionately more items than when with her naïve conspecific. Interestingly, although there is not a great deal of evidence, those naïve individuals that fared badly when foraging with a knowledgeable congener appeared to increase their proportion of prey taken over time. It is possible that they learnt which of the patches, not currently being utilised by their congener, contained food items and foraged there instead.

From the order of patch use by each individual in each trial, I was able to compare the frequency with which each individual followed another into a particular patch (i.e., joined another as that other foraged in the patch). For both species, naïve individuals followed knowledgeable ones significantly more frequently than the reverse ($p < 0.05$) and, anecdotally, although during trials 21 - 25, the first patch entered by naïve individuals was most often a poor patch that had previously been profitable, they soon began to initiate their searching in the most profitable patches (which were immediately occupied by the knowledgeable congener on release from the home enclosure).

Table 10.8: Mean number of follows for naïve and knowledgeable *S. fuscicollis* and *S. labiatus*.

	S. fuscicollis	***S. labiatus***
Naïve individual following a knowledgeable congener	28	30
Knowledgeable individual a following naïve congener	12	8

The presence of food was often vocally advertised, whether or not intentionally, by foraging individuals. That is, on first detecting food, the monkeys gave a distinctive food call which often brought their congeners over to the food. Although there was no increase in the food call rate of naïve or knowledgeable individuals with increasing patch quality (prey density) (Table 10.9), since knowledgeable individuals were most often the first to reach the rich patches (because they knew their location) they were also most often the first to encounter food and to food call in response to this. So it would appear that naive individuals of both species do attend to the behaviour (food calls) of their knowledgeable congeneric troop-mates and follow them to productive patches. However, individuals of the subordinate species upon entering these productive patches were then prevented from foraging freely in them by individuals of the dominant species. This is evident from the direction and total frequency of competitive interactions (food stealing, agonistic behaviour and displacements: see Table 4.5) in the different patches. 90 % of competitive interactions were directed from *S. labiatus* to *S. fuscicollis*, the majority of these occurring in the richer patches (Table 10.10).

Table 10.9: Total frequency of food calls by naïve and knowledgeable individuals (pooling species) in patches of different prey density.

	5 items	**10 items**	**15 items**	**Total**
Naïve individuals	12	9	11	32
Knowledgeable individuals	13	18	15	46

Table 10.10: Direction and total frequency of competitive interactions in patches of different prey density.

	0 items	**5 items**	**10 items**	**15 items**	**Total**
S. labiatus to *S. fuscicollis*	2	6	31	38	77
S. fuscicollis to *S. labiatus*	1	1	2	7	11

10.10 Discussion

As described in the introduction to this chapter, in the wild, within the home territory, individual tamarins can achieve maximum foraging success as a direct result of the intimate knowledge of the location of their resource patches and the productivity of these. Mixed-species troops may be advantageous if cross-species information transfer regarding this information can occur. By virtue of foraging in a cohesive social troop, individual tamarins may be able to benefit from the collective sampling experience of their congeners concerning the profitability of different food patches, by noting their foraging success in the different patches, and use this information to aid in patch quality assessment. In this way, both species may be able to save energy by following their congeners to productive fruiting trees in the separate strata and by avoiding unproductive ones without individually confirming resource depletion in the separate strata. Moreover, if individuals are able to use simple cues to judge the potential foraging success of others, and as a result preferentially follow or adopt the behaviour of their most successful troop mates, learning from others would become an extremely effective means of enhancing foraging efficiency (Wilkinson, 1992). Furthermore, as pointed out by Lachlan *et al.* (1998), the probability that no-longer-adaptive traits are transmitted in variable environments would be considerably reduced if observers chose demonstrators on the basis of their current success. The preferential following of successful foragers may also increase the speed with which advantageous patterns diffuse through a population.

On detecting food, both knowledgeable and naïve individuals of each species gave food calls. The universal, almost automatic, tendency for *S. fuscicollis* and *S. labiatus* to food call on sight of food (Prescott, pers. obs.) meant that it was not possible to examine if the tamarins use more subtle foraging behaviours as indicators of foraging success in addition to information that is donated through calls. As discussed in Chapter 9, food calls are thought to recruit troop-mates to the vicinity of the feeding individual, probably to facilitate the vigilance benefits accrued to cohesive troops (i.e., share the costs of predator vigilance) (Caine, 1993; Caine *et al.*, 1995). The cost of feeding competition incurred may be offset by this and by the prospect of future reciprocation regards the presence of food. However, in this experiment, the opportunity to observe and interact with a knowledgeable congener did not result in increased foraging efficiency for naïve individuals of both species due to asymmetry in dominance; the food patches being small enough to be aggressively defended and monopolised by the dominant *S. labiatus*. So although knowledgeable individuals (of both species) appear to advertise the presence of food with food calls which act to recruit troop mates to the vicinity of the food, if the knowledgeable individuals are of a dominant species to the follower, they will try to prevent the follower from exploiting the food. Tamarins foraging in social troops may thus be required to balance exclusive exploitation of any small, monopoliseable food patches they have discovered, against maintaining social contact and cohesion with the troop (for co-operative activities such as vigilance and care of infants).

Most field studies report little agonism (interference competition) between associating tamarin species (Pook & Pook, 1982; Peres, 1993b; Buchanan-Smith, 1990a; Heymann, 1990a). When inter-specific aggression does occur it is usually centred around disputes over food and is usually directed from members of the *S. mystax* group to *S. fuscicollis* (Pook & Pook, 1982; Buchanan-Smith, 1990a, for *S. fuscicollis* and *S. labiatus*; Heymann, 1990; Garber, 1988b, Peres, 1996, for *S. fuscicollis* and *S. mystax*; Terborgh, 1983, for *S. fuscicollis* and *S. imperator*). Peres (1996) writes that "*inter-specific social dominance should be expressed under conditions of limited feeding vacancies*" (p. 711), as was the case for the food patches in this experiment and all other experiments in this thesis. As has been observed in wild mixed-species troops (e.g., Hardie, 1998), *S. fuscicollis* were sometimes forced to wait outside a food patch until their congeners had terminated feeding in that patch and left. *S. fuscicollis* were never seen to exclude *S. labiatus* in this way, even if they were the first to enter the patch. Instead, the *S. fuscicollis* were either joined or evicted from the patch by *S. labiatus*.

Unfortunately, due to the territoriality of tamarins, and to the troops and time available for testing, I was unable to make the appropriate comparisons with performance when with a knowledgeable conspecific to negate this species confound. I expect that, for a naïve individual foraging with a knowledgeable conspecific, foraging efficiency would be increased. However, regardless of whether they are able to exploit the food patches, although naïve individuals were alerted to the location of the rich food patches by the food calls (and possibly other foraging behaviours) of their knowledgeable congeners and joined them at the food, I feel that they probably did not use this information to estimate relative patch quality. Rather, they probably simply remembered the location in which food was found and returned there. This may indirectly lead to increased foraging efficiency through exploitation of the rich patches but without any conscious estimate of patch quality. Such social learning of food location, rather than food patch quality, would be adaptive in a mixed-species context as described in Chapter 9. The costs of sharing food may be quite small if the food patches are large, ephemeral, or if there is a future benefit to sharing through anticipated future reciprocation. Although, in small groups or pairs, it may be possible for individuals to observe the foraging success of other individuals simultaneously exploiting a patch, for food items that can be processed and swallowed quickly (i.e., food items with short handling times) or in densely vegetated habitats, it is probably difficult for individuals to assess precisely the foraging success of others from observation of their foraging behaviour because, under such circumstances, the quality of visual information transferred is degraded. Moreover, any experimental investigation of foraging or learning that assures a large number of trials overlooks the fact that animals do not always have this number of chances to perfect or match their behaviour in natural situations.

10.11 Conclusion

In conclusion, the experiments contained in this chapter investigated the way in which tamarins respond to variations in the distribution and density of their food; this being important in helping to understand how their behaviour is adapted to ensure efficient foraging generally. The major food resources of tamarins (ripe fruit and insects) are spatially and temporally heterogeneous. Heterogeneity may pose problems for foraging decision-makers because it can introduce uncertainty. The ability to assess environmental heterogeneity accurately is expected to influence fitness. Single-species pairs of *S. fuscicollis* and *S. labiatus* were found to discriminate between feeding patches of varying quality (prey density) and to distribute their search effort accordingly, thereby increasing their foraging efficiency. The monkeys had a tendency to continue to sample poor quality patches (including patches containing no food) having learnt the distribution of prey density amongst patches. Sampling and exploitation of previously unproductive food patches can lower the current rate of feeding but may still be selectively advantageous in the long term as a strategy to acquire information to maintain future foraging success in the face of environmental variability. Both species readily learned to associate patch quality with particular patch locations (i.e., they showed excellent spatial memory for the location of high quality patches) and rapidly learned the new locations of high quality patches following a switch in prey density distribution. The monkeys showed no evidence of associating patch quality with local visual cues (red ribbons). This may have been due to perceptual difficulties or to poor experimental design, rather than an innate species characteristic. In mixed-species pairs, with each species possessing divergent knowledge concerning patch quality, foraging efficiency was found to be reduced by the presence of a dominant knowledgeable congener (due to patch monopolisation) but may be increased by the presence of a subordinate one. Information transferred between individuals through food calls, and possibly other foraging behaviours, probably concerned simply the location at which food was available rather than relative patch quality.

These experiments were severely limited by sample size. For example, considering Experiment 10, with an n of only four animals per role (naïve and knowledgeable), it is obviously difficult to get statistically significant results unless there is very low variability within each role. The experiments do at least demonstrate that the testing methodology is sound (although more detailed observations of individual foraging behaviour may have cast light upon the types of information available for transfer) and that it is possible to investigate the free-foraging behaviour of tamarins in a free-ranging naturalistic environment. One must, however, have an appreciation of the perceptual abilities of individual foragers.

The experiments were also limited by the unavailability of familiar, related conspecifics. This meant that Experiment 10 was confounded by having mixed-species male and female pair design. Thus the species differences observed may have actually been sex differences, which may or may not be a result of different colour vision. It would have been interesting to repeat the experiments with single-species troops or mixed-species troops of four individuals to investigate whether an increase in troop size increases or decreases foraging efficiency. However, aside from this being precluded by the troop available for study, four individuals is probably too many monkeys for one observer to observe simultaneously in the 'Free-Range Area'.

Chapter 11

General Discussion

"Researchers whose work on social learning is part of a broader interest in animal behaviour or behavioural ecology more often study social learning to understand the role of social interactions in the development of patterns of behaviour that enhance the fitness of free-living animals."

[Galef, 1996a: p. 3]

11.1 The Operation of Social Learning About Food in Tamarin Mixed-Species Troops

The broad aim of this thesis was to explore the foraging behaviour of single-species and mixed-species troops of *S. fuscicollis weddelli* and *S. labiatus labiatus* in order to further understanding of the function of tamarin mixed-species troops in general and how social learning may play an adaptive role within them. Relatively few learning studies have focused on social influences on the development, diffusion and transmission of learned behaviours in ways that inform us about the contributions of social learning to the fitness of group living animals. The thesis also sought to evaluate the biological and behavioural differences between the species that permit their association.

Tamarin mixed-species troops are formed between *S. fuscicollis* and each of the three members of the *S. mystax* group (*S. mystax*, *S. labiatus*, *S. imperator*) in all areas where they are sympatric. The remarkable stability and permanency of such troops, in comparison to most other primate mixed-species troops, has led to the proposal of numerous hypotheses concerning their adaptive advantage (see Heymann & Buchanan-Smith, submitted). These are not fundamentally different from those explaining the evolution of intra-specific gregariousness in animals in general (e.g., Bertram, 1978) and can be categorised into those decreasing the risk of predation, those increasing foraging efficiency and those improving resource defence. Such hypotheses are extremely difficult to test in the wild for a number of reasons, not least because the stability and permanency of tamarin mixed-species troops means that participating species are rarely found out of association. Implicit in many of these hypotheses is the notion of inter-specific information transfer through social learning. Gathering of evidence for social learning is also difficult in the wild because detailed observations must be made at so close a distance as to be unambiguous of interpretation. This is particularly difficult for tamarins because their heavily vegetated forest environment, small body size and sometimes timid nature precludes such observations. Nor can one control for previous experience in the wild. Therefore, it is difficult to prove the exact contribution of any social influence on learning because individuals may have had many opportunities to learn independently. To circumvent these problems, I studied social learning in captive single-species and mixed-species troops of *S. fuscicollis weddelli* and *S. labiatus labiatus* in a unique set up at Belfast Zoological Gardens. Tests were made of one group of hypotheses, the foraging benefit hypotheses, which propose that individuals in mixed-species troops may increase their foraging efficiency either as a result of increased troop size in mixed-species troops or as a result of species divergence in behaviour. Social learning, defined in this thesis as 'learning from others or having one's learning influenced by others', is universally implicated in the framework of many of the foraging benefit hypotheses (e.g., guiding, sharing or parasitism of knowledge). However, there is, as yet, little empirical evidence for it in tamarin mixed-species troops. Consequently, the experiments in this thesis involved investigations of social learning of different types of food-related information. Empirical evidence for such social learning in captivity would strengthen the hypotheses that suggest that increased opportunity for social learning is an adaptive advantage of mixed-species troop formation in tamarins. As outlined in Chapter 3, there are a number of reasons as to why one might expect social learning to play an important role in how these monkeys respond to food related challenges in both single-species and in mixed-species troops. For example, they live in close-knit, stable family troops characterised by a high degree of co-operation, cohesion and tolerance (Caine, 1993). Tamarin troops also co-operate inter-specifically, with associating species also showing a high degree of cohesion and tolerance. High levels of co-operation, cohesion and tolerance leads to increased proximity and increased frequency of interaction, both of which are likely to favour social learning. However, as pointed out by Fragaszy and Visalberghi (1996), although intense sociality provides ample occasion for social learning, it does not necessarily produce it. One must consider also what learning demands are faced by individual tamarins within their social troops. In fact, their diverse diet (and the patchy nature of their food) is likely to present them with a plethora of food related challenges, the solutions to which may be acquired by social learning. These may include learning the wide range of palatable food items that comprises their diverse diet in the first instance, learning how to hunt and overcome the physical and chemical defences of their insect and vertebrate prey, learning how to acquire their plant resources and the significance of cues indicating the ripeness of these, and learning the location in which particular food patches are found and the optimal pattern of exploitation of these.

The learning abilities of individual tamarins were investigated then in ecologically relevant learning experiments involving foraging tasks that bear relation to these problems typically faced by tamarins foraging in the wild. The experiments were mostly either of a within-subject design (where comparisons were made between individuals in single-species troops with those same individuals in mixed-species troops to examine the direct effect of the presence of a congener on the behaviour of particular individuals) or a between-subject design (where comparisons were made between single-species troops containing the same number of individuals as the combined number of both species in an analogous mixed-species troop). Individuals were always tested in the presence of at least one other individual.

It was found that social interaction facilitated learning by individual tamarins of the method of acquisition of food on a novel foraging task, the palatability of a particular food type, and the location of food distributed within their environment. Furthermore, this social learning was rapid. It is widely accepted that the ability to learn from others is an important adaptation that allows animals to acquire information important for survival (adaptive behaviours) at low cost (e.g., Galef, 1976; Bateson, 1988; Plotkin, 1988). For example, according to laboratory learning paradigms, the trial and error processes necessary for asocial acquisition of adaptive patterns of behaviour are often both energy consuming and error-filled undertakings for the acquirer. Social learning provides an alternative, often optimal, route to asocial learning by allowing animals to learn about their environments more rapidly, uniformly and effectively, without making costly mistakes or wasting time on exploration (Galef, 1976, 1995). Social learning can also help young animals incorporate into their behavioural repertoires the learned adaptive (rewarding) behaviour of their more experienced adult conspecifics through some process less cumbersome or dangerous than *de novo* trial and error learning and can help adult animals monitor, track and deal with the ebb and flow of resources in (not too rapidly) changing environments more quickly and efficiently than they could do so alone (Galef, 1993, 1996b).

Later experiments examined the response of tamarins to variability in the spatial and temporal distribution of food within their environment and how association affects this response. The results of these experiments drew attention to the critical impact the distribution of food has on foraging efficiency and to the sensitivity of foraging tamarins to this. This sensitivity was found to be a product of both asocial and social learning in that the tamarins individually sampled food patches within their environment, probably to acquire information for use in future foraging decisions, but were also found to learn from a congener the new patch locations at which food was available following a temporal change in its spatial distribution.

It is further proposed that facilitation of social learning about various types of food-related information is likely to be an advantage of mixed-species troop formation in wild tamarins. Because both species in most experiments were found to learn from their congeners equally as well as they learnt from their conspecifics, this means that an increase in troop size, as a result of mixed-species troop formation, will thus increase the opportunity for information transfer between individuals accordingly. Furthermore, again given that both species learn from their congeners as well as their conspecifics, if participating species in mixed-species troops are in any way divergent in their foraging behaviour or knowledge of food, then mixed-species troops may be advantageous over single-species troops in that both species may potentially be able to take advantage of an increased knowledge base (i.e., the knowledge of their own species and that of their congeners) concerning food related information. Divergent knowledge regards food is probable for associating tamarin species because of the vertical segregation between them. In the wild, *S. fuscicollis* are found to occupy a lower height in the forest than *S. labiatus*. This means that the species are likely to have specialist knowledge regarding food resources in the separate strata. In experiments in which each species was given divergent knowledge about food location or distribution, both species were found to respond to the food finds of their congener (although they did not then learn from them the *type* of location in which food was to be found or relative patch quality). So mixed-species troops may indeed be additionally advantageous in that vertical segregation may lead to an increased probability of detecting food resources.

In all cases of inter-specific social learning, both species were found to learn from each other equally as well, so any advantage accrued through social learning in mixed-species troops is likely to be symmetrical. However, as is the case in the wild, *S. labiatus* were found to be dominant over *S. fuscicollis* and this meant that *S. fuscicollis* were often unable to take advantage of any information that they had gained through social learning. Nevertheless, the demonstration that *S. fuscicollis* and *S. labiatus* in mixed-species troops in captivity can learn from each other about various types of food related information strengthens the hypotheses that suggest that social learning about food is an adaptive advantage of mixed-species troop formation in wild tamarins.

Having said that, the captive environment can never be entirely indicative of the wild and one must exercise caution in drawing conclusions between proximate influences on behaviour in captivity and functional and proximate influences on behaviour in the wild. Experimental evidence that a particular factor can influence the behaviour of individuals in captivity does not necessarily mean that the factor does influence the behaviour of individuals in the wild. The captive mixed-species troops at the zoo were observed to exhibit behaviours typical of their wild counterparts (e.g., the dominance of *S. fuscicollis* over *S. labiatus*; the greater willingness of *S. fuscicollis* to descend to low levels; differences in insect foraging styles) which lends support to the generalisation of the experimental results to wild tamarin mixed-species associations. However, wild tamarins may not forage in as close proximity as did the tamarins in the captive experiments and this may act to decrease the probability of social learning through observation of the behaviours of others. Also, in the rain forest, tree canopies are so dense that visual cues are typically ineffective beyond 10 - 15 metres (Garber, 1989). Thus, the densely vegetated rain forest habitat of tamarins may also preclude social learning through observation over much of the day. Furthermore, associated tamarin species often show parallel, as distinct from integrated, progression through the forest and this pattern of movement is not optimal for inter-specific observational learning. For information typically transmitted through vocal signals (e.g., the presence of a predator or an abundant food resource: Heymann, 1987; Buchanan-Smith, 1990a; Caine, 1993; Caine *et al.*, 1995), these factors are not a problem. Associating tamarin species can be found within 20 - 50 metres of each other for around 83 % of their daily activity period (Buchanan-Smith, 1990a, for *S. fuscicollis* and *S. labiatus*; Heymann, 1990a; Peres, 1992b; Smith, 1997, for *S. fuscicollis* and *S. mystax*). At such distances, individuals can almost certainly hear and respond to the vocal signals (e.g., alarm or food calls) of their troop-mates. Thus the benefits arising through association from social learning remain viable when information is transmitted through the auditory modality. Neither do general guiding effects require detailed observation on the part of the follower and here the presence of food may be communicated by speed of movement in addition to vocal signals.

For information transmission that is dependent upon detailed observation (e.g., the learning of novel feeding techniques or the palatability of different food types), close proximity may indeed be necessary. However, when feeding on fruit resources, associating tamarin species often show simultaneous use of nearby trees of the same resource species or, at large non-monopolisable resources, feed within the same tree (Terborgh, 1983; Peres, 1996). When foraging for insects, mean inter-individual distances are typically 1 - 10 metres (Garber, 1980; Yoneda, 1984b; Soini, 1987; Peres, 1992b). Therefore, although clear, detailed observation may be made difficult by obstructing vegetation, opportunity for observation remains. With regards the grasping strategy required for the heavy pendulous pods of *Parkia* and many other pod-like or small-sized fruit resources commonly taken by tamarins (e.g., *Inga* spp., *Brosimum* spp., *Pourouma* spp., *Cecropia* spp.), because of their position on long thin stalks in the periphery of the tree crown, the component behaviours necessary to reach them can be expected to be more visible than those for exploitation of large fruits or perhaps insect prey. Social learning by infants is almost certainly not constrained by poor visibility since tamarin infants are carried for the first 10 - 12 weeks of life. This means that they are able to attend extremely closely to the interactions of their carriers with food.

With the exception of some ornithological studies, such as those by Krebs (1973) and Rubenstein *et al.* (1977), most laboratory studies of social learning phenomena have examined learning within species and not between species. This thesis goes someway towards redressing this imbalance and, to my knowledge, is unique in providing examples of inter-specific social learning between two mammal species (excluding humans). The importance of the evidence gathered for intra- and inter-specific social learning in tamarins in captivity lies in the fact that huge assumptions are made regards the benefits species gain from group living but very few studies actually test these. For example, it has long been proposed that tamarins gain anti-predatory advantages from forming mixed-species troops. However, until Hardie and Buchanan-Smith (1997) and Peres (1993a) quantified vigilance benefits to individuals in captivity and in the wild respectively, the proposition remained simply an unsubstantiated assumption.

The proposition that associated tamarin species gain foraging benefits through learning from each other was largely untested until this thesis. I suggest that, given the evidence presented in this thesis for social learning about food in captivity, and given the social environment of tamarins in the wild, this proposition is a sound one. Troop members tend to be highly synchronous within and between species during resting, travelling, insect foraging and when feeding in superabundant plant resource patches (Peres, 1996). Membership in a cohesive troop and performing most essential activities as a co-ordinated unit, would provide a mechanism whereby essential survival information can be efficiently transmitted between troop members. When one member of a troop is feeding, the rest of the troop is generally feeding too, often in the same tree. Simply by virtue of belonging to a social troop, and doing what other members of the troop are doing, individuals are provided with the opportunity to learn, say, what is palatable or safe to eat (following a change in ecological conditions or for novel foods). In this way, social learning allows individuals to track environmental variability more efficiently than does asocial learning alone as social learners can quickly and safely home in on appropriate behaviour by sharing up to date foraging information (Laland *et al.*, 1993). Similarly, foraging in a co-ordinated, cohesive troop can support the learning of particular feeding skills or methods of acquisition of food from other troop members. The social interaction with others increases the opportunity for an individual to encounter the appropriate environmental stimuli and/or provides models of the behaviours required to acquire the food. Membership in a kin-related, cohesive social unit, utilising the same supplying area over successive generations, may also greatly enhance efficient foraging by serving to transmit information on the types and distribution patterns or preferred foods to new generations of kin (Milton, 1981). A general guiding effect arising from inter-specific cohesion may also be important for associating species to learn not only the location of food, what are likely places to search for food and optimal travel routes, but also food palatability since the mere presence of a conspecific or congener at a food site may influence food choice.

Although primarily concerned with the functional significance of social learning within tamarin mixed-species troops, rather than the precise mechanisms involved, we have a pattern emerging regarding the learning mechanisms at work. Social learning of foraging information can proceed along routes of varying complexity but what we appear to have from the experimental results contained in this thesis is evidence of simple low level mechanisms, where individuals are influenced in their own learning by social interaction in quite simple ways. Most of the facilitation of learning appeared a result of an individual being attracted by another to a particular stimulus (stimulus enhancement) or locality (local enhancement) within the environment. This is perhaps unsurprising since it has been reported elsewhere that, in most instances, transmission of behaviour in non-human primates appears to result, in the large part, from the introduction of one individual of another into a stimulus situation in which the second is predisposed either as a result of previous experience or instinctive tendency to respond in such a way as to acquire the behaviour of the first (e.g., Whiten & Ham, 1992; Fragaszy & Visalberghi, 1996). However, Experiment 1 provided evidence that, in addition to a simple stimulus enhancement effect, observer animals may have learnt something from the manipulation of the foraging task apparatus by the demonstrator which lead to a matching response on the task. However, the observed matching was probably due to some kind of facilitation of existing behavioural responses (response facilitation) as opposed to the acquisition of novel ones (imitation). In general, as illustrated above, social learning in tamarins probably need not proceed by complex mechanisms or require advanced cognitive abilities in order to be adaptive in natural populations. In fact, in view of the possible constraints on visual contact in the wild, within and particularly between species, which may limit the opportunity for the exchange of information through detailed observation, it may be that the more simple the learning mechanism the better. That is, simple low-level learning mechanisms may not only be sufficient but optimal.

Of course individuals can learn about food asocially, but the important point is that it is thought to be additionally advantageous to have the ability to learn socially also. However, social learning is often considered to be less adaptive than individual learning in rapidly changing environments because traits can continue to be transmitted after they are no longer optimal (Boyd & Richerson, 1985, 1988). Laland *et al.* (1993) suggest that, in such environments (spatially and temporally variable environments), strong social learning will only occur in a social foraging situation provided there are regular "reality checks" through individual learning. It is interesting in this context, that the tamarins persisted in sampling poor food patches in Experiments 8, 9 and 10, after having learnt the distribution of the poor and high quality patches probably, in part, due to the influence of their troop-mates.

Animals that survive on patchily distributed resources are likely to be under considerable selective pressure to diversify their diet and to show dietary flexibility (Milton, 1981). Tamarins consume a wide variety of highly dispersed, patchily distributed, and often seasonal, food resources (e.g., insects, small vertebrates, ripe fruit, plant exudates and nectar) and are amongst the most opportunistic feeders of living primates. In order to exploit a wide range of seasonal food resources, dietary generalists must maintain sufficient behavioural plasticity to permit the development of appropriate feeding techniques (Weigl & Hanson, 1980). Both social and asocial learning are forms of behavioural plasticity enabling animals to acquire behaviours that are adaptive in their local habitat (Boyd & Richerson, 1988). One may expect these to play supplementary or complementary roles in behavioural development depending upon the costs and benefits that make one or other superior in any given environmental situation.

So individual tamarins can learn from their conspecifics and congeners about food and, in as much as an ability to learn socially as well as asocially is adaptive, this likely constitutes an advantage of mixed-species troop formation since an increase in troop size as a result of association will increase the opportunity for information transfer accordingly. Many of the benefits ascribed for mixed-species troops (including foraging, anti-predatory, and resource defence benefits) are simply a consequence of increased troop size. However, mixed-species troops may be advantageous over single-species troops in that feeding competition is ordinarily less severe between species than within (and thus individuals in mixed-species troops may accrue the benefits of increased troop size without incurring the increased feeding competition they would suffer in a similarly sized single-species troop). This is thought to be the case for associating tamarin species. Fieldwork data, collected in the Pando Department of north-western Bolivia, provided corroborative evidence of divergence in forest utilisation in wild mixed-species troops of *S. fuscicollis* and *S. labiatus*. For example, *S. fuscicollis* was found to locomote primarily by vertical clinging and leaping between large-sized, vertically orientated substrates in the forest understory. Whereas, *S. labiatus* locomoted more by quadrapedal walking and running upon, and leaping between, small, horizontal and oblique substrates in the forest canopy. This divergence is a reflection of the general behavioural and morphological specialisation to separate forest strata seen in these species. For example, despite consuming similar plant based diets, the species are characterised by different prey foraging strategies and exploit different types of insect prey from the different strata (Garber, 1993a). Such divergence, together with related differences in body size, probably permits co-existence in mixed-species troops by limiting the negative effect of inter-specific feeding competition on troop stability and cohesion. As described earlier, adaptation to separate strata may also increase the potential for the foraging (and anti-predatory) benefits accrued to associating species in mixed-species troops.

In Experiment 4, *S. fuscicollis* demonstrated a willingness to descend to near the ground in their enclosure and this facilitated *S. labiatus* to do the same in their presence. As such, this is a possible asymmetric advantage of mixed-species troops to *S. labiatus* in that they may be more able to investigate and (given their dominance over *S. fuscicollis*) utilise potentially beneficial objects occurring in this area in the presence of *S. fuscicollis*. In the experiments investigating social learning, no differences were found in the probability or speed of learning between species, so any benefit accrued from social learning would appear to be symmetrical between species. However, *S. fuscicollis* were sometimes prevented from capitalising upon food-related information gained through social learning. This was because, in most experiments, food was distributed in small, monopoliseable, spatially restricted food patches. Access to the food was thus largely a function of whether each species could withhold its feeding position within a patch. This, in turn, depended on inter-specific status: the larger bodied *S. labiatus* were always dominant over the smaller *S. fuscicollis*, which were excluded or displaced from the food resources, irrespective of the number of conspecifics involved in a contest. This is reported to be the case for *S. fuscicollis* with *S. labiatus* in the wild too (Buchanan-Smith, 1990a), and for *S. fuscicollis* with *S. mystax* (Heymann, 1990b; Peres, 1996) and with *S. imperator* (Terborgh, 1983). The finding illustrates the point that the costs of association may be greater to *S. fuscicollis* in terms of displacement at monopoliseable feeding sites due to their subordinate status (interference competition) (but note that Peres (1991) reports that large, *non-monopoliseable* patches account for most of the feeding time of *S. fuscicollis* and *S. mystax* in association). However, the benefits to *S. fuscicollis* in association may be greater also. For example, in mixed-species troops of *S. fuscicollis* and *S. mystax*, *S. mystax* invest more in vigilance and territorial defence than do *S. fuscicollis* and *S. mystax* flush insects to lower levels for capture by *S. fuscicollis*: see Table 2.1). Yet, although there may be asymmetry in the costs and benefits to each species (and individuals) in mixed-species troops, the overall effect of association is seemingly beneficial to both species. Asymmetric cost-benefit trade-offs should not undermine the evolution and maintenance of mixed-species troops so long as the integrated benefits exceed the costs to individuals of either species independently of one another. Presumably, the benefits from association outweigh the costs and, on balance, the fitness gains are sufficiently large to constitute a strong enough selective advantage to have affected the species over an evolutionary time scale to favour association. Mixed-species troops may thus represent an evolutionary stable strategy (Maynard-Smith, 1982). However, comparing species pairings, one can predict that the overall benefits are greatest for *S. fuscicollis/S. mystax* who spend the greatest amount of time in association. There is good evidence that both foraging efficiency benefits and anti-predator benefits apply to this association (Peres, 1992b, 1993a, 1996), but possibly only the latter to *S. fuscicollis/S. imperator* associations (Terborgh, 1983), and to a smaller degree given that the stability of association is less and degree of food overlap lower.

11.2 Limitations, Improvements and Future Research

I was invited to explore the foraging benefit hypotheses proposed for wild tamarin mixed-species troops. However, the functional explanations proposed for the evolution of these troops (e.g., improved predator detection, improved foraging efficiency, improved resource defence) are neither conflicting nor mutually exclusive. Indeed, these advantages appear to be closely related to one another and to distinctive features of each species' ecology. For instance, the ecological and morphological adaptation of associating tamarin species to different forest strata allows the mixed-species troop to scan for different predators at different heights and to search for food patches in the different strata all at once. In fact, anti-predator considerations may impose constraints on tamarin foraging behaviour in general. For example, it is possible that tamarins cut short their foraging time in order to travel to safe sleeping sites before dusk (Moynihan, 1970; Caine, 1987). Thus it is far from ideal to examine the hypotheses in isolation when they are likely to form part of a complex cost-benefit analysis. Moreover, as already mentioned, the costs and benefits may be different for each species and for individuals within each species. Nevertheless, examining the hypotheses in isolation can help refine or adapt them, or aid in the generation of new ones, even if it does not allow their ultimate confirmation or rejection.

Furthermore, that hetero-specific troop living promotes an ultimate overall adaptive advantage to participating individuals can only be shown conclusively by quantifying the performance, in terms of survival and fecundity, of individuals in both single-species troops and mixed-species troops under comparable environmental conditions. Therefore, there is an obvious need for long-term studies of such troops in the wild to verify that association is advantageous and to establish the fundamental fitness currencies involved. In this regard, it would be interesting to investigate asymmetry in the costs and benefits of association for individuals, according to their age, sex or social status, because of the different selective forces acting upon them. Similarly, we have little detailed information about the adaptive advantages of social learning generally, or about its influence on the reproductive success and inclusive fitness of individuals of different species. This too would require detailed, long-term field studies.

Long-term developmental studies are also necessary in order to specify in more detail exactly what learning demands are faced by individual tamarins in their natural habitat and how these demands are overcome. For example, we know very little about the rate at which infant tamarins sample novel foods, or about the exact nature of the physical and chemical defences of the insect prey taken by tamarins. If social learning does not play an important role under natural circumstances, it would be an academic exercise to examine it in captivity. It is thus necessary to examine the frequency and importance of phenomena suggestive of behavioural transmission in natural environment. Such information may have particular interest in view of the possible differences in the costs and benefits to different individuals in mixed-species troops. These long-term studies represent difficult but not impossible topics for further research.

The facilities at Belfast Zoological Gardens were excellent and the zoo provided a large number of monkeys for testing. However, some experiments were limited by sample size. For example, for Experiments 8, 9 and 10, it was possible to house only two single-species pairs of each species on the 'Free-Range Area' per summer, because of the logistics involved in relocating the animals and the need for habituation to the free-ranging environment. Those experiments conducted in the 'Old Marmoset-House' and 'End-Enclosure' that were of a between-subjects design were also limited by sample size in that it was not possible to match the sex, age and troop composition of all mixed-species troops with those of a similarly sized single-species troop because of a lack of large family troops. Single-species troops of an appropriate size for comparison could not be created simply by combining a number of single-species pairs due to the possibility of extreme aggression between unfamiliar, unrelated conspecifics.

For Experiments 2 and 3, it would have been possible to increase sample size by repeating the entire protocol for each mixed-species troop, but changing the roles of the participants (i.e., where *S. labiatus* learned the aversion, now *S. fuscicollis* do so). However, this would have required using two additional food types and the results of a food-preference test found it difficult to identify additional suitable and strongly favoured food types, for which it was possible to induce an aversion toward. Role reversal was not possible for Experiment 1 either because it investigated responses to novel apparatus. Nor was it possible to increase sample size by using a single knowledgeable pair (Experiment 1) or non-averse pair (Experiments 2 and 3) for interaction with all naïve pairs (Experiment 1) or all averse pairs (Experiments 2 and 3) because of the effects of experience and because of the possibility of aggression between unfamiliar, unrelated conspecifics. If the available sample size of large family troops had been greater it may have been possible to compare large single-species troops with smaller ones to investigate further the effects of an increase in troop size on the facilitation of social learning or to explore transmission further with a transmission chain design as used by Laland and Plotkin (1990).

The experimental results presented in this thesis showed evidence of considerable variation between individuals within troops in terms of their learning ability. For example, in Experiment 1, the latency with which observers completed the novel foraging task after observation ranged from 25 seconds to over 4 hours. However, a caveat to all experiments in this thesis is that, should an individual fail to show evidence of learning on a particular task at a particular time, this does not mean that the individual has not learnt the appropriate information to succeed on the task. Marked individual (and sex) differences have been found elsewhere for tamarins in vigilance, in exploration of new territories, in dispersal, and in feeding. These may occur because selection favours the adoption of different strategies by different individuals or because of the effects of experience on behaviour. Although individual differences are an important phenomenon in their own right, they can overwhelm or blur consistent species differences. For tamarins, differences in performance between individuals may also be related to the colour vision capabilities of the individuals involved. The application of genotype analysis would help in understanding what discriminations individuals having particular colour vision phenotypes can make, especially comparisons between dichromatic and trichromatic females alone (i.e., avoiding sex-based confounds). Work done in this regard by myself (Buchanan-Smith *et al.*, unpubl. MS) has found dichromatic *S. fuscicollis* and *S. labiatus* individuals to be at a disadvantage in fruit detection and selection relative to trichromats. In fact, no other study has focused upon how variation in colour vision affects behaviour and dealings with the natural environment (e.g., fruit feeding, detection of predators). Clearly, further research is needed to see how closely colour vision capacity is matched to the crucial discriminations required to obtain a suitable diet and to avoid predators. An appreciation of the colour vision phenotypes of particular captive study animals is also crucial with regards appropriate experimental design.

Individual differences in performance in investigations of social learning are observed not only because of differences between the individuals themselves but also because of the differing relations between particular dyadic interactants. We must learn more about the circumstances that influence and direct the establishment, strength and persistence of relationships among individual tamarins since these will govern attention, proximity and behavioural homogeny and therefore ultimately opportunities for social learning. Undoubtedly, the ages, sex, status, parity, relatedness and temperament of troop members, as well as food availability, season, and other ecological variables, affect, how, when, and if tamarins respond to conspecifics and congeners in the wild and hence the direction (i.e., who learns from whom) and frequency of social learning. We must also investigate the types of social influences individuals can have on each other (e.g., arousing, motivating, inhibiting or disinhibiting), not only through overt behaviour (e.g., fear responses) but also through mere presence.

Another obvious candidate for further research is investigation of precisely what social cues and signals are used in information transfer of food-related information between individuals and what is communicated. Also, as described in Chapter 10, if individuals are able to use simple cues to judge the potential foraging success of others, and as a result preferentially follow or adopt the behaviour of their most successful troop mates, learning from others would become an extremely effective means for enhancing foraging efficiency. So how do individuals recognise successful foragers? The vocal repertoire of callitrichines is as relatively highly developed as other forest primates (Moody and Menzel, 1976; Cleveland & Snowdon, 1982; Snowdon & Soini, 1988). Certainly the presence or location of food is communicated by characteristic food calls in both species (e.g., Moody & Menzel, 1976; Caine *et al.*, 1995; this study). Thus, it may be possible that successful foragers are identified by the rate at which they food call. Food calls might convey information over and above the simple food presence. For example, Caine *et al.* (1995) carefully noted the different contexts in which food calls were given and found that, for *S. labiatus*, food calls are given more often for abundant and rare food resources. Careful and repeated observation of the context in which particular signals, auditory or otherwise, are given will likely lead to the formation of hypotheses regards their function. These hypotheses can then be tested by isolating and experimentally manipulating (e.g., reducing, exaggerating, deleting, or changing the context of) the relevant candidates. Playback experiments, like those of Windfelder (1997) investigating the response of associated and non-associated *S. fuscicollis* and *S. imperator* to playback of the long call vocalisations of their conspecific and congeneric troop members, and of Olupot *et al.* (1998) investigating the response of *L. albigena* to the calls of sympatric frugivores, may also help in examining auditory communication. Examining communication in other modalities which are less easily manipulated and whose signals are less easily reproduced will be more difficult.

Compared to other simian primates, callitrichines have a limited repertoire of behavioural responsiveness as in overt facial and body postures (Box, 1991), no doubt, in part, to their habitat which precludes close inspection of each other's visual signals over much of the day. So visual signals may play a less important role in efficient foraging than do auditory signals. However, the scent marking behaviour of the Callitrichinae is regarded as the most elaborately developed of the simian primates and they have highly developed olfactory sensory systems (e.g., Epple *et al.*, 1993). Given that they typically depend on olfactory communication in socio-sexual contexts, it is possible that salient information about food is also communicated between individual tamarins through olfaction. Heymann (1991) observed that scent marking by wild *S. mystax* is concentrated at feeding trees. Scent marking of such resources may communicate information regarding their nature. For example, in *Callithrix* and *Cebuella*, which obtain much of their diet by gouging holes into the bark of trees and consuming exudate, scent marking is concentrated at gouge holes (Lacher *et al.*, 1981; Rylands, 1985; Stevenson & Rylands, 1988). Lacher *et al.* found that several troops of *C. penicillata* (black-tufted ear marmoset) fed from and scent marked the same sap holes. This led these authors to suggest that scent located at sap holes may inform individual animals about the time elapsed since the last utilisation of the holes and therefore about the availability of sap (as well as playing a territorial role in helping to prevent the meeting of several troops at the same time). However, Rylands (1985) and Stevenson and Rylands (1988) consider scent marking at gouging holes to be primarily related to intra-troop communication since such localities are highly likely to be sniffed by all members of the troop. Olfactory cues from ripening fruit almost certainly play an important role in locating these resources in addition to spatial knowledge from possible cognitive maps (Garber, 1989).

Given the patchy distribution of their food, spatial knowledge is probably extremely important to tamarins and their spatial memory appears well developed. However, debate exists as to how this spatial memory is organised. In order to forage efficiently tamarins must learn not only the location of food patches but also the optimum travel routes between them. Cognitive mapping has been suggested as the mechanism underlying the complex learning and memory processes associated with the efficient foraging observed for tamarins, primarily on the strength of evidence for straight line, goal directed travel and a low incidence of backtracking between feeding trees (Garber, 1989; Garber & Hannon, 1993). Yet, to prove the existence of true co-ordinate based cognitive maps, as opposed to merely a remote set of pathways among known landmarks, critical experiments are needed which confirm that novel short-cuts are truly novel and that the study animals are not simply using routes by recognising a series of familiar landmarks and moving towards them (Bennet, 1996). These experiments are essentially impossible in wild populations because usually one cannot control all the available resources within a given test area sufficiently to allow firm conclusions about which mechanism guide spatial movements and one often does not know the location and renewal rates of all potential resources within the test area until these have been visited by the study animals. However, Garber and Dolins (1996) have gone some way towards addressing this issue for tamarins with controlled field experiments.

11.3 Final Comment

In closing, the very nature of the question I was invited to explore (i.e., whether individual tamarins accrue foraging benefits through mixed-species troop formation) necessitates examination of behaviour in the wild. This is because to show that mixed-species troop formation facilitates social learning about food in captive mixed-species troops does not necessarily mean that it does so in wild mixed-species troops; only that there is a real possibility for it to do so. That is all that it was possible to demonstrate under the circumstances. However, as stated earlier, this is still very important. As ever though, long-term, detailed field observations of well-habituated individuals/troops and rigorous field experiments are needed to confirm the operation and adaptive advantage of social learning about food in wild troops. Following the Bolivian expedition, I fully appreciate the difficulties inherent in following and observing unhabituated troops of these small, habitually cryptic monkeys in the dense secondary growth of the South American rain forest. But until evidence is collected from wild populations, increased frequency of social learning as an advantage of mixed-species troop formation in tamarins remains a hypothesis, albeit a more secure one. As with all research into the behavioural biology of natural processes, it is particularly useful to carry out co-ordinated and complementary programmes of investigation in the laboratory and in the field (Box, 1991). Thus, the nature of this type of research is cyclic. The captive work helps confirm, reject, refine or adapt the surmised functional hypotheses for mixed-species troops, and aids in the generation of new ones, for re-examination back in the wild.

References

Abbot, D.H., Barret, J., & George, L.M. (1993). Comparative aspects of the social suppression of reproduction in female marmosets and tamarins. In A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology* (pp. 152-162). Oxford: Oxford University Press.

Adams-Curtis, L.E., & Fragaszy, D.M. (1995). Influence of a skilled model on the behaviour of conspecific observers in tufted capuchin monkeys (*Cebus apella*). *American Journal of Primatology, 37*, 65-71.

Addington, R.L. (1992). *Food calls and group foraging in red-bellied tamarins.* Unpublished M.Sc. thesis, Bucknell Univeristy, Lewisburg, Pennsylvania.

Alcock, J. (1969). Observational learning by fork-tailed flycatchers. *Animal Behaviour, 17*, 652-657.

Alexander, R.D. (1974). The evolution of social behaviour. *Annual Reviews of Ecology and Systematics, 5*, 323-383.

Allen, J.R. (1986). The influence of species composition on behaviour in mixed-species cyprinid shoals. *Journal of Fish Biology, 29 (Suppl. A)*, 97-106.

Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour, 49*, 227-267.

Altmann, S.A. (1974). Baboons, space, time and energy. *American Zoologist, 14*, 221-248.

Andrews, M.W., & Rosenblum, L.A. (1995). Location effects of social partner on experimental foraging in the squirrel monkey. *American Journal of Primatology, 36*, 175-183.

Assersohn, C., & Whiten, A. (1998). *Development of foraging and food sharing in chimpanzees of the Budongo Forest, Uganda.* Abstract published in the proceedings of the XVIIth IPS Congress, Antananarivo, Madagascar.

Attenborough, D. (1995). *The Private Life of Plants: A natural history of plant behaviour.* London: BBC Books.

Axelrod, R., & Hamilton, W.D. (1981). The evolution of cooperation. *Science, 211*, 1390-1396.

Ayres, J.M. & Clutton-Brock, T.H. (1992). River boundaries and species range size in Amazonian primates. *American Naturalist, 140*, 531-537.

Baker, A.J. (1991). *Evolution of the social system of the golden lion tamarin* (Leontopithecus rosalia)*: Mating system, group dynamics, and cooperative breeding*. Unpublished Ph.D. thesis, University of Maryland, College Park.

Baker, H.G., & Baker, I. (1975). Studies of nectar constitution and pollinator-plant coevolution. In L.E. Gilbert & P.H. Raven (Eds.), *Coevolution of animals and plants* (pp. 100-140). Austin: University of Texas Press.

Baker, H.G., & Baker, I. (1983). A brief historical review of the chemsitry of floral nectar. In B. Bentley & T. Elias (Eds.), *Biology of Nectaries* (pp. 126-152). New York: Columbia University Press.

Baker, M.C., Belcher, C.S., Deutsch, L.C., Sherman, G.L., & Thompson, D.B. (1981). Foraging success in junco flocks and the effects of social hierarchy. *Animal Behaviour, 29*, 137-142.

Bartecki, U., & Heymann, E.W. (1987). Field observation of snake-mobbing in a group of saddle-back tamarins, *Saguinus fuscicollis nigrifrons*. *Folia Primatolgica, 48*, 199-202.

Bateson, P.P.G. (1988). The active role of behaviour in evolution. In M.W. Ho & S. Fox (Eds.), *Evolutionary Processes and Metaphors* (pp. 191-207). Chichester, UK: Wiley.

Beauchamp, G., & Kacelnik, A. (1991). Effects of the knowledge of partners on learning rates in zebra finches *Taeniopygia guttata. Animal Behaviour, 41*, 247-253.

Belwood, J.J. (1990). Anti-predator defences and ecology of neotropical katydids, especially the Pseudophyllinae. In W. Bailey & D.C.F. Rentz (Eds.), *The Tettigoniidae: Biology, systematics and evolution* (pp. 8-26). Berlin: Springer Verlag.

Bennet, A.T.D. (1996). Do animals have cognitive maps? *Journal of Experimental Biology, 199*, 219-224.

Bernstein, I.S. (1967). Intertaxa interactions in a Malayan primate community. *Folia Primatologica, 7*, 198-207.

Bertram, B.C. (1978). Living in groups. In J.R. Krebs & N.B. Davies (Eds.), *Behavioural Ecology* (pp. 64-96). Sunderland, MA: Sinauer Associates.

Boinski, S., & Fragaszy, D.M. (1989). The ontogeny of foraging in squirrel monkeys (*Saimiri oerstedi*). *Animal Behaviour, 37*, 415-428.

Boissinot, S., Zhou,Y.-H., Qiu, L., & Dulai, K.S. (1997). Origin and molecular evolution of the X-linked duplicate color vision genes in howler monkeys. *Zoological Studies, 36*, 360-369.

Bourlière, F. (1985). Primate communities: their structure and role in tropical ecosystems. *International Journal of Primatology, 6*, 1-26.

Box, H.O. (1984). *Primate Behaviour and Social Ecology*. London: Chapman & Hall.

Box, H.O. (1991). Responsiveness to environmental change: Interrelationships among parameters. In H.O Box (Ed.) *Primate Responses to Environmental Change* (pp. 57-73). London: Chapman & Hall.

Box, H.O. (1997). Foraging strategies among male and female marmosets and tamarins (Callitrichidae): New perspectives in an underexplored area. *Folia Primatologica, 68*, 296-306.

Box, H.O., Röhrhuber, B., & Smith, P. (1995). Female tamarins (*Saguinus* - Callitrichidae) feed more successfully than males in unfamiliar foraging tasks. *Behavioural Processes, 34*, 3-12.

Boyd, R., & Richerson, P.J. (1985). *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.

Boyd, R., & Richerson, P.J. (1988). An evolutionary model of social learning: the effects of spatial and temporal variation. In T.R. Zentall & B.G. Galef (Eds.), *Social Learning: Psychological and biological perspectives* (pp. 29-48). Hillsdale, New Jersey: Lawrence Erlbaum.

Bradbury, J.W. (1975). Social organization and communication. In W. Wimsatt (Ed.), *Biology of Bats, Vol. 3* (pp. 1-72). New York: Academic Press.

Brady, R.H. (1979). Natural selection and the criteria by which a theory is judged. *Systematic Zoology, 28*, 600-621.

Brown, A.D., & Rumiz, D.I., (1986). Distibución y conservacion de los Primates en Bolivia - estado actual de su conocimiento. In M.T. de Mello (Ed.), *A primatologia no Brasil-2* (pp. 335-363). Brasília: Sociedade Brasilieira de Primatologia.

Brown, G.S., & Gass, C.L. (1993). Spatial association learning by hummingbirds. *Animal Behaviour, 46*, 487-497.

Brown, K., & Mack, D.S. (1978). Food sharing among captive *Leontopithecus rosalia. Folia Primatologica, 29*, 268-290.

Bshary, R. & Noë, R. (1997). Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behaviour, 54*, 1461-1474.

Buchanan-Smith, H.M. (1989). *The social organisation and mating system of the red bellied tamarins (*Saguinus labiatus labiatus*); Behavioural observations in captivity and in the wild.* Unpublished Ph.D. thesis, University of Reading, Reading.

Buchanan-Smith, H.M. (1990a). Polyspecific association of two tamarin species, *Saguinus labiatus* and *Saguinus fuscicollis*, in Bolivia. *American Journal of Primatology, 22*, 205-214.

Buchanan-Smith, H.M. (1990b). Observations of Gray's bald face saki, *Pitheca i. irrorata*, in Bolivia. *Regional (U.K.) Studbook for the white-faced saki* Pitheca p. pitheca, *2*, 2-8.

Buchanan-Smith, H.M. (1991a). A field study of the red-bellied tamarin, *S. l. labiatus*, in Bolivia. *International Journal of Primatology, 12*, 259-276.

Buchanan-Smith, H.M. (1991b). Encounters between neighbouring groups of tamarins in northern Bolivia. *Primate Report, 31*, 95-99.

Buchanan-Smith, H.M. (1999). Tamarin polyspecific associations: Forest utilization and stability of mixed-species groups. *Primates, 40*, 233-247.

Buchanan-Smith, H.M. (in press). Exploration of unfamiliar areas and detection of potentially threatening objects in single- and mixed-species groups of tamarins. *International Journal of Comparative Psychology*.

Buchanan-Smith, H.M., & Hardie, S.M. (1997). Tamarin mixed-species groups: An evaluation of a combined captive and field approach. *Folia Primatologica, 68*, 272-286.

Buchanan-Smith, H.M., Hardie, S.M., Prescott, M.J., Stronge, J., & Challis, M. (1996). Callitrichids at Belfast Zoological Gardens, Northern Ireland. *Neotropical Primates, 4*, 143-146.

Buchanan-Smith, H.M., Caceres, C., Hardie, S.M. & Prescott, M.J. (in prep). Distribution and forest utilisation of *Saguinus* and other primates of the Pando Department, Northern Bolivia.

Buchanan-Smith, H.M., Mundy, N., & Prescott, M.J. (unpubl. MS). The functional utility of colour vision: Effects of ploymorphism on behaviour in callitrichines.

Bugnyar, T., & Huber, L. (1997). Push or pull: an experimental study on imitation in marmosets. *Animal Behaviour, 54*, 817-831.

Byrne, R.W. (1994). The evolution of intelligence. In P.J.B. Slater & T.R. Halliday (Eds.), *Behaviour and Evolution* (pp. 223-265). Cambridge: Cambridge University Press.

Byrne, R.W. (1995). *The Thinking Ape: Evolutionary origins of intelligence.* Oxford: Oxford University Press.

Caine, N.G. (1984). Visual scanning by tamarins: a description of the behaviour and tests of two derived hypotheses. *Folia Primatologica, 43*, 59-67.

Caine, N.G. (1987). Vigilance, vocalisations and cryptic behaviour at retirement in captive groups of red bellied tamarins (*Saguinus labiatus). American Journal of Primatology, 12*, 241-250.

Caine, N.G. (1990). Unrecognized antipredator behaviour can bias observational data. *Animal Behaviour, 39*, 195-197.

Caine, N.G. (1993). Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: the role of predation pressures. In A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology* (pp. 200-219). Oxford: Oxford University Press.

Caine, N.G., & Stevens, C. (1990). Evidence for a 'monitoring' call in captive red-bellied tamarins. *American Journal of Primatology, 22*, 251-262.

Caine, N.G., Potter, M.P., & Mayer, K.E. (1992). Sleeping site selection by captive tamarins (*Saguinus labiatus*). *Ethology, 90*, 63-71.

Caine, N.G., Addington, R.L., & Windfelder, T.L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour, 50*, 53-60.

Cambefort, J.P. (1981). Comparative study of culturally transmitted patterns of feeding habits in the Chacma baboon (*Papio ursinus*) and the vervet monkey (*Cercopithecus aethiops*). *Folia Primatologica, 36*, 243-263.

Cameron, R., & Buchanan-Smith, H. (1992). Primates of the Pando, Bolivia. *Primate Conservation, 12-13*, 11-14.

Cameron, R., Wiltshire, C., Foley, C., Dougherty, N., Aramayo, X., & Rea, L. (1989). Goeldi's monkey and other primates of northern Bolivia. *Primate Conservation, 10*, 62-70.

Cant, J.G.H., & Temerin, L.A. (1984). A conceptual approach to foraging adaptations in primates. In P.S. Rodman & J.G.H. Cant (Eds.), *Adaptations for Foraging in Nonhuman Primates* (pp. 304-342). New York: Columbia University Press.

Caraco, T. (1979). Time budgeting and group size: a test of theory. *Ecology, 60*, 618-627.

Caraco, T. (1980). On foraging time allocation in a stochastic environment. *Ecology, 61*: 119-128.

Caraco, T. (1981a). Risk-sensitivity and foraging groups. *Ecology, 62*, 119-128.

Caraco, T. (1981b). Energy budgets, risk and foraging preferences in dark eyed juncos (*Junco hyemalis*). *Behavioural Ecology and Sociobiology, 8*, 213-217.

Caraco, T., Martindale, S., & Whittam, T.S. (1980a). An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour, 28*, 820-830.

Caraco, T., Martindale, S., & Pulliam, H.R. (1980b). Avian flocking in the presence of a predator. *Nature, 285*, 400-401.

Castro, C.N.R. (1991). *Behavioural ecology of two coexisting tamarin species (*Saguinus fuscicollis nigrifrons *and* Saguinus mystax mystax, *Callitrichidae, Primates) in Amazonian Peru.* Unpublished Ph.D. thesis, Washington University, St. Louis.

Castro, R., & Soini, P. (1978). Field studies on *Saguinus mystax* and other callitrichids Amazonian Peru. In D.G. Kleiman (Ed.), *Biology and Conservation of the Callitrichidae* (pp. 73-78). Washington D.C.: Smithsonian Institution Press.

Chamove A.S., & Anderson, J.R. (1989). Examining environmental enrichment. In E. F. Segal (Ed.), *Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates*. Park Ridge, New Jersey: Noyes Publications.

Chamove, A.S., Hosey, G.R., & Schaetzel, P. (1988). Visitors excite primates in zoos. *Zoo Biology, 7*, 359-369.

Charles-Dominique, P. (1977). *Ecology and Behaviour of Nocturnal Primates*. New York: Columbia University.

Cheney, D., & Wrangham, R. (1987). Predation. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate Societies* (pp. 34-43). Chicago: University of Chicago Press.

Chivers, D.J. (1977). The feeding behaviour of the siamang (*Symphalangus syndactylus*). In T.H. Clutton-Brock (Ed.), *Primate Ecology: Studies in feeding and ranging behaviour in lemurs, monkeys and apes* (pp. 355-382). London: Academic Press.

Christen, A., & Geissmann, T. (1994). A primate survey in northern Bolivia, with special reference to Goeldi's monkey, *Callimico goeldii. International Journal of Primatology, 15*, 239-274.

Clark, A.B. (1991). Individual variation in responsiveness to environmental change. In H.O Box (Ed.) *Primate Responses to Environmental Change* (pp. 91-109). London: Chapman & Hall.

Clark, C.W., & Mangel, M. (1984). Foraging and flocking strategies: Infromation in an uncertain environment. *American Naturalist, 123*, 626-641.

Clark, C.W., & Mangel, M. (1986). The evolutionary advantages of group foraging. *Theoretical Population Biology, 30*, 45-75.

Cleveland, J., & Snowdon, C.T. (1982). The complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). *Zeitschrift für Tierpsychologie, 58*, 231-270.

Cleveland, J., & Snowdon, C.T. (1984). Social development during the first twenty weeks in the cotton-top tamarin (*Saguinus o. oedipus*). *Animal Behaviour, 32*, 432-445.

Clutton-Brock, T.H., & Harvey, P.H. (1976). Evolutionary rules and primate societies. In P.P.G. Bateson & R.A. Hinde (Eds.), *Growing Points in Ethology*. Cambridge: Cambridge University Press.

Clutton-Brock, T.H., & Harvey, P.H. (1977a). Primate ecology and social organization. *Journal of Zoology, London, 183*, 1-39.

Clutton-Brock, T.H., & Harvey, P.H. (1977b). Species differences in feeding and ranging behaviour in primates. In T.H. Clutton-Brock (Ed.), *Primate Ecology: Studies in feeding and ranging behaviour in lemurs, monkeys and apes* (pp. 557-584). London: Academic Press.

Clutton-Brock, T.H., & Harvey, P.H. (1980). Primates, brains and ecology. *Journal of Zoology, London, 190*, 309-323.

Coates, A., & Poole, T.B. (1983). The behaviour of the callitrichid monkey, *Saguinus labiatus*, in the laboratory. *International Journal of Primatology, 4*, 339-371.

Cody, M.L. (1971). Finch flocks in the Mohave Desert. *Theoretical Population Biology, 2*, 142-158.

Coimbra-Filho, A.F. & Mittermeier, R.A. (1976). Exudate-eating and tree gouging in marmosets. *Nature, 262*, 630.

Coimbra-Filho, A.F., & Mittermeier, R.A. (1977). Conservation of the Brazilian lion tamarins (*Leontopithecus rosalia*). In H.S.H. Prince Rainier III of Monaco & G.H. Bourne (Eds.), *Primate Conservation* (pp. 59-94). New York: Academic Press.

Coimbra-Filho, A.F., & Mittermeier, R.A. (1978). Tree-gouging, exudate eating and the "short-tusked" condition in *Callithrix* and *Cebuella*. In D.G. Kleiman (Ed.), *Biology and Conservation of the Callitrichidae* (pp. 23-27). Washington D.C.: Smithsonian Institution Press.

Colinvaux, P. (1978). *Why Big Fierce Animals Are Rare: An ecologist's perspective.* Princeton, New Jersey: Princeton University Press.

Commons, M.L., Herrnstein, R.J., Rachlin, H. (1982).*Quantitative Analyses of Behaviour, Vol. 2: Matching and maximising accounts*. Cambridge, Massachusetts: Ballinger Publishing Company.

Coombe, B.G. (1976). The development of fleshy fruit. *Annual Review of Plant Physiology, 27*, 207-228.

Cords, M. (1987). Mixed-species association of Cercopithecus monkeys in the Kakamega Forest, Kenya. *University of California Publications in Biology, Vol 117*, 1-109.

Cords, M. (1990). Mixed-species association of East African guenons: general patterns or specific examples? *American Journal of Primatology, 21*, 101-114.

Coussi-Korbel, S., & Fragaszy, D.M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour, 50*, 1441-1453.

Crandlemire-Sacco, J.L. (1986). *The ecology of the saddle-backed tamarin,* S. fuscicollis, *of southeastern Peru.* Unpublished Ph.D. thesis, University of Pittsburgh, Pittsburgh.

Crook, J.H. (1965). The adaptive significance of avian social organisations. *Symposia of the Zoological Society of London, 14*, 181-121.

Crook, J.H. (1970). The socio-ecology of primates. In J.H. Crook (Ed.), *Social Behaviour in Birds and Mammals* (pp. 103-166). London: Academic Press.

Crook, J.H. (1972). Sexual selection, dimorphism, and social organization in the primates. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man. 1871-1971* (pp. 231-281). Chicago: Aldine.

Crook, J.H., & Gartlan, J.S. (1966). Evolution of primate societies. *Nature, 210*, 1200-1203.

Curio, E. (1976). *The Ethology of Predation*. Berlin: Springer-Verlag.

Cuthill, I.C., Kacelnik, A., Krebs, J.R., Haccou, P., & Iwasa, Y. (1990). Starlings exploiting patches: the effect of recent experience on foraging decisions. *Animal Behaviour, 40*, 625-640.

Darwin, C. (1892). *The Origin of Species by Means of Natural Selection*. London: John Murray.

Dawkins, R. (1989). *The Selfish Gene*. Oxford: Oxford University Press.

Dawson, B.V., & Foss, B.M. (1965). Observational learning in budgerigars. *Animal Behaviour, 13*, 470-474.

Dawson, G.A. (1976). *Behavioural ecology of the Panamanian tamarin,* Saguinus oedipus *(Callitrichidae, Primates)*. University Microfilms International, Ann Arbor.

Dawson, G.A. (1978). Composition and stability of social groups of the tamarin, Saguinus oedipus geoffroyi, in Panama: ecological and behavioural implications. In D.G. Kleiman (Ed.) *Biology and Conservation of the Callitrichidae*, (pp. 23-37). Washington, D.C.: Smithsonian Institution Press.

Dawson, G.A. (1979). The use of time and space by the Panamanian tamrain, *Saguinus geoffroyi. Folia Primatologica, 31*, 253-284.

Debrot, A.O., & Myreberg, A.A. (1988). Intraspecific avoidance as a proximate cause for mixed-species shoaling by juveniles of a western Atlantic surgeonfish. *Bulletin of Marine Science, 43*, 104-106.

Diamond, J.M. (1978). Niche shifts and the rediscovery of interspecific competition. *American Scientist, 66*, 322-331.

Dolins, F. (1993). *Spatial relational learning and foraging in cotton-top tamarins*. Unpublished Ph.D. thesis, University of Stirling.

Drea, C.M., & Wallen, K. (1995). Gradual acquisition of visual discrimination tasks in a social group of rhesus monkeys (*Macaca mulatta*). *Animal Learning and Behavior, 23*, 1-8.

Dunbar, R.I.M. (1988). *Primate Social Systems*. London: Croom Helm.

Edwards, P.J., & Wratten, S.D. (1980). *Ecology of Insect-Plant Interactions*. London: Edward Arnold.

Eguchi, K., Yamagishi, S., & Randriansolo, V. (1993). The composition and foraging behaviour of mixed-species flocks of forest living birds in Madagascar. *Ibis, 135*, 91-96.

Ehrlich, P.R., & Ehrlich, A.H. (1973). Coevolution: heterotypic schooling of Carribean reef fiches. *American Naturalist, 107*, 157-160.

Eisenberg, J.F. (1978). Comparative ecology and reproduction of New World Monkeys. In D.G. Kleiman (Ed.), *Biology and Conservation of the Callitrichidae* (pp. 13-22). Washington, D.C.: Smithsonian Institution Press.

Eisenberg, J.F. (1989). *Mammals of the Neotropics, Vol. 1: The northern neotropics*. Chicago: Chicago University Press.

Eisenberg. J.F., Muckenhirn, N.A., & Rudran, R. (1972). The relation between ecology and social structure in primates. *Science, 176*, 863-874.

Elgar, M.A. (1989). Predator avoidance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Review, 64*, 13-33.

Elner, R.W., & Hughes, R.N. (1978). Energy maximization in the diet of the shore crab *Carcinus maenas*. *Journal of Animal Ecology, 49*, 271-276.

Emlen, S.T., & Vehrencamp, S.L. (1985). Cooperative breeding strategies among birds. In B. Holldobbler & M. Lindauer (Eds.), *Forschritte der Zoologie, Vol. 31* (pp. 359-374). Stuttgart: G. Fisher.

Emmons, L.H. (1980). Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecological Monographs, 50*, 31-54.

Emmons, L.H. (1987). Comparative feeding ecology of felids in a neotropical rainforest. *Behavioural Ecology and Sociobiology, 20,* 271-283.

Encarnación, F. (1990). *Informe 01/90 Sub-proyecto: Investigacion y manejo de Saguinus labiatus en el sur oriente del Perú.* Unpublished report, Proyecto Peruano de Primatologia 'Manuel Moro Sommo', Iquitos. 12 pp.

Epple, G. (1971). Discrimination of the odor of males and females by the marmoset *Saguinus fuscicollis* spp. *Proceedings of the 3rd International Congress of Primatology, Zurich, 1970, Vol. 3.* (pp. 166-171). Basel: Karger.

Epple, G. (1973). The role of pheromones in the social communication of marmoset monkeys (Callitrichidae). *Journal of Reproduction and Fertility Suppl. 19*, 447-454.

Epple, G. (1974a). Olfactory communication in South American primates. *Annals of the New York Academy of Sciences, 237*, 261-278.

Epple, G. (1974b). Pheromones in primate reproduction and social behavior. In W. Montagna & W.A. Sadler (Eds.), *Reproductive Behavior* (pp. 131-155). New York: Plenum Press.

Epple, G. (1975a). The behaviour of marmoset monkeys (Callitrichidae). In L.A. Rosenblum (Ed.), *Primate Behaviour, Vol. 4* (pp. 195-239). New York: Academic Press.

Epple, G. (1975b). Parental behaviour in *Saguinus fuscicollis* spp. (Callitrichidae). *Folia Primatologica, 24*, 221-238.

Epple, G. (1978a). Reproductive and social behaviour of marmosets with special reference to captive breeding. *Primate Medicine, 10*, 50-62.

Epple, G. (1978b). Studies on the nature of chemical signals in scent marks and urine of *Saguinus fuscicollis*. *Journal of Chemical Ecology, 4*, 383-394.

Epple, G. (1978c). Notes on the establishment and maintenance of the pair bond in *Saguinus fuscicollis*. In D.G. Kleiman (Ed.), *The Biology and Conservation of the Callitrichidae*. Washington, D.C.: Smithsonian Institution Press.

Epple, G., & Katz, Y. (1980). Social influences on first reproductive success and related behaviors in the saddle-back tamarin (*Saguinus fuscicollis*, Callitrichidae). *International Journal of Primatology, 1*, 171-183.

Epple, G., & Katz, Y. (1984). Social influences on estrogen secretion excretion and ovarian cyclicity in saddle-back tamarins (*Saguinus fuscicollis*). *American Journal of Primatology, 6*, 215-227.

Epple, G., Alveraio, M.C., Golob, N.F., & Smith, A.B., III (1980). Stability and a attractiveness related to age of scent-marks of saddle-back tamarins (*Saguinus fuscicollis*). *Journal of Chemical Ecology, 6*, 735-748.

Epple, G., Alveario, M.C., Belcher, A.M., & Smith, A.B., III. (1987). Species and subspecies specificity in urine and scent marks of saddle-back tamarins (*Saguinus fuscicollis*). *International Journal of Primatology, 8*, 663-680.

Epple, G., Belcher, A.M., Kudërling, I., Zeller, U., Scolnick, L., Greenfield, K.L., & Smith, A.B. III., (1993). Making sense out of scents: species differences in scent glands, scent-marking behaviour, a scent-mark composition in the Callitrichidae. In A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology* (pp. 123-151). Oxford: Oxford University Press.

Estrada, A. (1984). Resource use by howler monkeys (*Alouatta palliata*) in the rain forest of Los Tuxtlas, Veracruz, Mexico. *International Journal of Primatology, 5*, 105-132.

Fairbanks, L. (1975). Communication of food quality in captive *Macaca nemestrina* and free-ranging *Ateles geoffroyi. Primates, 16*, 181-189.

Feistner, A.T.C. (1985). *Food-Sharing in the Cotton-Top Tamarin,* Saguinus oedipus oedipus. Unpublished M.Sc. thesis, University of Stirling, Stirling.

Feistner, A.T.C., & Chamove, A.S. (1986). High motivation toward food increases food sharing in cotton-top tamarins. *Developmental Psychobiology, 19*, 439-452.

Feistner, A.T.C., & McGrew, W.C. (1989). Food-sharing in primates: A critical review. In P.K. Seth & S. Seth (Eds.), *Perspectives in Primate Biology, Vol. 3* (pp. 21-36). New Delhi: Today and Tomorrow's Printers and Publishers.

Feistner, A.T.C., & Price, E.C. (1990). Food-sharing in cotton-top tamarins (*Saguinus oedipus*). *Folia Primatologica, 54*, 34-45.

Feistner, A.T.C., & Price, E.C. (1991). Food offering in New World primates: Two species added. *Folia Primatologica, 57*, 165-168.

Ferrari, S.F. (1988). *Social behaviour in* Callithrix flaviceps*: An ecological perspective.* Paper presented at the Workshop on Monogamy in the Callitrichidae, University of Gottingen, Gottingen, 26-28th February, 1988.

Ferrari, S.F. (1992). The care of infants in a wild marmoset (*Callithrix flaviceps*) group. *American Journal of Primatology, 26*, 109-118.

Ferrari, S.F. (1993). Ecological differentiation in the Callitrichidae. In A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology*. Oxford: Oxford University Press.

Ferrari, S.F., & Lopes Ferrari, M.A. (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, S.F., & Lopes Ferrari, M.A. (1990a). Predator avoidance behaviour in the buffy-headed marmoset, *Callithrix flaviceps*. *Primates, 31*, 323-338.

Ferrari, S.F., & Lopes Ferrari, M.A. (1990b). A survey of primates in central Pará. *Bol. Mus. Para. Emilio Goeldi, ser. Zool., 6*, 169-179.

Ferrari, S.F., & Lopes Ferrari, M.A. (1992). New data on the distribution of primates in the region of the confluence of the Jiparana and Madeira Amazonas in Rondônia, Brazil. *Goeldiana Zoologica, Numero 11, 31 de Janeiro de 1992.*

Ferrari, S.F., & Martins, E.S. (1992). Gummivory and gut morphology in two sympatric callitichids (*Callithrix emiliae* and *Saguinus fuscicollis weddelli*) from western Brazilian Amazonia. *American Journal of Physical Anthropology, 88*, 97-103.

Fitzgibbon, C.D. (1990). Mixed-species grouping in Thompson's and Grant's gazelles: the antipredator benefits. *Animal Behaviour, 39*, 1116-1126.

Fleagle, J.G. (1980). Locomotion and posture. In D. Chivers (Ed.), *Malayan Forest Primates: Ten years' study in tropical rain forest* (pp. 191-208). New York: Plenum Press.

Fleagle, J.G. (1988). *Primate Adaptation and Evolution*. London: Academic Press.

Fleagle, J.G., & Mittermeier, R.A. (1980). Locomotor behavior, body size and comparative ecology of seven Suriname monkeys. *American Journal of Physical Anthropology, 52*, 301-304.

Fleagle, J.G., Mittermeier, R.A., & Skopec, A.L. (1981). Differential habitat use by *Cebus apella* and *Saimiri sciureus* in central Surinam. *American Journal of Physical Anthropology, 54*, 219-220.

Ford, S.M. (1980). Callitrichids as phyletic dwarfs, and the place of the Callitrichidae in the Platyrrhini. *Primates, 21*, 31-43.

Ford, S.M. (1986). Systematics of the New World monkeys. In D. Swindler & J. Erwin (Eds.), *Comparative Primate Biology, Vol. 1, Systematics, evolution and anatomy* (pp. 73-135). New York: Alan R. Liss.

Fragaszy, D.M., & Box, H.O. (1986). Primate behaviour and cognition in nature. In J.G Else & P.C. Lee (Eds.), *Primate Ontogeny, Cognition and Social Behaviour* (pp. 73-78). Cambridge University Press, Cambridge.

Fragaszy, D.M., & Visalberghi, E. (1990). Social processes affecting the appearance of innovative behaviours in capuchin monkeys. *Folia Primatologica, 54*, 155-165.

Fragaszy, D.M., & Visalberghi, E. (1996). Social learning in monkeys: Primate "primacy" reconsidered. In C.M. Heyes & B.G. Galef, Jr. (Eds.), *Social Learning in Animals: The roots of culture* (pp. 65-85). London: Academic Press.

Freeland, W.J. (1977). Blood-sucking flies and primate polyspecific associations. *Nature, 269*, 801-802.

Freeman, C.E., Worthington, R.D., & Corral, R.D. (1985). Some floral nectar-sugar compositions from Durango and Sinaloa, Mexico. *Biotropica, 17*, 309-313.

Freese, C.H., Freese, M.A., & Castro, R.N. (1978). The status of the callitrichids in Peru. In D.G. Kleiman (Ed.), *Biology and Conservation of the Callitrichidae* (pp 121-130). Washington, D.C.: Smithsonian Institution Press.

Freese, C.H., Heltne, P.G., Castro, R.N., & Whitesides, G. (1982). Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. *International Journal of Primatology, 3*, 53-90.

French, J.A. (1987). Reproductive suppresssion in marmosets and tamarins: Absence of social effects in the lion tamarin (*Leontopithecus rosalia*). *American Journal of Primatology, 12*, 342.

French, J.A., Abbott, D.H., & Snowdon, C.T. (1984). The effect of social environment on estrogen secretion, scent-marking, and socio-sexual behaviour in tamarins (*Saguinus oedipus*). *American Journal of Primatology, 6*, 155-167.

Galef, B.G., Jr. (1976). Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. In J.S. Rosenblatt, R.A. Hinde, E. Shaw & C. Beer (Eds.), *Advances in the Study of Behavior, Vol. 6* (pp. 77-100). New York: Academic Press.

Galef, B.G., Jr. (1986). Social interaction modifies learned aversions, sodium appetite, and both palatability and handling-time induced dietary preferences in rats (*Rattus norvegicus*). *Journal of Comparative Psychology, 100*, 432-439.

Galef, B.G., Jr. (1988). Imitation in animals: history, definition and interpretation of data from the psychological laboratory. In T.R. Zentall & B.G. Galef (Eds.), *Social Learning: Psychological and biological perspectives* (pp. 3-28). Hillsdale, New Jersey: Erlbaum.

Galef, B.G., Jr. (1990). Tradition in animals: field observation and laboratory analyses. In M. Bekoff, & D. Jamieson (Eds.), *Methods, Inference, Interpretation and Explanation in the Study of Behavior* (pp. 74-95). Boulder, Colorado: Westview Press.

Galef, B.G., Jr. (1993). Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission. *Animal Behaviour, 46*, 257-265.

Galef, B.G., Jr. (1995). Why behaviour patterns that animals learn socially are locally adaptive. *Animal Behaviour*, 49, 1325-1334.

Galef, B.G., Jr. (1996a). Social learning and imitation. In C.M. Heyes & B.G. Galef, Jr. (Eds.), *Social Learning in Animals: The roots of culture* (pp. 3-15). London: Academic Press.

Galef, B.G., Jr. (1996b). Social influences on food preferences and feeding behaviors of vertebrates. In E.D. Capaldi (Ed.), *Why we eat what we eat: The psychology of eating* (pp. 207-231). Washington, D.C.: American Psychological Association.

Galef, B.G., Jr. (1996c). The adaptive value of social learning: a reply to Laland. *Animal Behaviour, 52*, 641-644.

Galef, B.G., Mittermeier, R.A., & Bailey, R.C. (1976). Predation by tayra (*Eira barbara*). *Journal of Mammology, 54*, 152-154.

Garber, P.A. (1980). Locomotor behaviour and feeding ecology of the Panamanian Tamarin (*Saguinus oedipus geoffroyi*, Callitrichidae, Primates). *International Journal of Primatology, 1*, 185-201.

Garber, P.A. (1984a). Use of habitat and positional behavior in a neotropical primate, *Saguinus oedipus*. In P. Rodman & J. Cant (Eds.), *Adaptations for Foraging in Nonhuman Primates* (pp. 112-133). New York: Columbia University Press.

Garber, P.A. (1984b). Proposed nutritional importance of plant exudates in the diet of the Panamanian tamarin, *Saguinus oedipus geoffroyi*. *International Journal of Primatology*, 5, 1-15.

Garber, P.A. (1986). The ecology of seed dispersal in two species of callitrichid primates (*Saguinus mystax* and *S. fuscicollis*). *American Journal of Primatology, 10*, 155-170.

Garber, P.A. (1987). Foraging strategies among living primates. *Annual Review of Anthropology, 16*, 339-364.

Garber, P.A. (1988a). Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichidae, Primates) in Amazonian Peru. *Biotropica, 20*, 100-106.

Garber, P.A. (1988b). Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. *Behaviour, 105*, 18-34.

Garber, P.A. (1989). Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. *American Journal of Primatology, 19*, 203, 216.

Garber, P.A. (1991). A comparative study of positional behaviour in three species of tamarin monkeys. *Primates, 32*, 219-230.

Garber, P.A. (1992). Vertical clinging, small body size and the evolution of feeding adaptations in the Callitrichinae. *American Journal of Physical Anthropology, 88*, 469-482.

Garber, P.A. (1993a). Feeding ecology and behaviour of the genus *Saguinus*. In A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology* (pp. 273-295). Oxford: Oxford University Press.

Garber, P.A. (1993b). Seasonal patterns of diet and ranging in two species of tamarin monkeys: stability versus variability. *International Journal of Primatology, 14*, 145-166.

Garber, P.A., & Dolins, F.L. (1996). Testing learning paradigms in the field: Evidence for use of spatial and perceptual information and rule-based foraging in wild moustached tamarins. In M. Norconk, A.L. Rosenberger, & P.A. Garber (Eds.), *Adaptive Radiations of Neotropical Primates* (pp. 201-216) New York: Plenum Press.

Garber, P.A., & Hannon, B. (1993). Modeling monkeys: A comparison of computer-generated and naturally occurring foraging patterns in two species of neotropical primates. *International Journal of Primatology, 14*, 827-852.

Garber, P.A., & Leigh, S.R. (1997). Ontogenic variation in small-bodied New World primates: Implications for patterns of reproduction and infant care. *Folia Primatologica, 68*, 1-22.

Garber, P.A., & Paciulli, L.M. (1997). Experimental field study of spatial memory and learning in wild capuchin monkeys (*Cebus capucinus*). *Folia Primatologica, 68*, 236-253.

Garber, P.A., & Pruetz, J.D. (1995). Positional behavior in moustached tamarin monkeys: Effects of habitat on locomotor variability and locomotor stability. *Journal of Human Evolution, 28*, 411-426.

Garber, P.A., & Teaford, M.F. (1986). Body weights in mixed-species troops of *Saguinus mystax* and *Saguinus fuscicollis nigrifrons* in Amazonian Peru. *American Journal of Physical Anthropology, 71*, 331-336.

Garber, P.A., Moya, L., & Malaga, C. (1984). A preliminary 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, P.A., Moya, L., Encarnación, F., & Pruetz, J. (1991). Demography, patterns of dispersal, and polyandrous matings in an island population of moustached tamarin monkeys. *American Journal of Primatology, 24*, 102. (Abstract).

Garber, P.A., Encarnación, F., Moya, L., & Pruetz, J.D. (1993a). Demographic and reproductive patterns in moustached tamarin monkeys (*Saguinus mystax*): Implications for reconstructing platyrrhine mating systems. *American Journal of Primatology, 29*, 235-254.

Garber, P.A., Pruetz, J.D., & Isaacson, J. (1993b). Patterns of range use, range defense, and intergroup spacing in moustached tamarin monkeys (*Saguinus mystax*). *Primates, 34*, 11-25.

Garcia, J.E, & Cases, V. (1989). El estado de la primatologia en Bolivia. *Boletin Primatológico Latinamericano, 1*, 21-35.

Gartlan, J.S., & Struhsaker, T.T. (1972). Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa. *Journal of Zoology, London, 168*, 221-266.

Gause, G.F. (1934). *The Struggle for Existence.* New York: Hafner.

Gautier, J.P., & Gautier-Hion, A. (1969). Les associations polyspécifiques chez les Cercopithecidae du Gabon. *Terre et Vie, 2*, 164-201.

Gautier-Hion, A. (1978). Food niches and coexistence in sympatric primates in Gabon. In D.J. Chivers & J. Herbert (Eds.), *Recent Advances in Primatology, Vol. 1, Behaviour* (pp. 269-286). New York: Academic Press.

Gautier-Hion, A. (1980). Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *Journal of Animal Ecology, 49*, 237-269.

Gautier-Hion, A. (1988). Polyspecific associations among forest guenons: ecological, behavioural and evolutionary aspects. In A. Gautier-Hion, F. Bourlière, J.P. Gautier & K. Kingdon (Eds.), *Primate Radiation: Evolutionary biology of the African guenons* (pp. 452-476). Cambridge: Cambridge University Press.

Gautier-Hion, A., & Gautier, J.P. (1974). Les associations polyspécifiques de Cercopithèques du Plateau de M'passa (Gabon). *Folia Primatologica, 22*, 134-177.

Gautier-Hion, A., & Tutin, C.E.G. (1988). Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Folia Primatologica,* 51, 149-151.

Gautier-Hion, A., Quris, R., & Gautier, J. (1983). Monospecific vs polyspecific life: A comparative study of foraging and antipredatory tactics in a community of *Cercopithecus* monkeys. *Behavioural Ecology and Sociobiology, 12*, 325-335.

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C., and Thiollay, J.-M. (1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia, 65*, 324-337.

Gill, F., & Wolf, L. (1977). Non-random foraging by sunbirds in a patchy environment. *Ecology, 58*, 1284-1296.

Giraldeau, L.-A., & Lefebvre, L. (1987). Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Animal Behaviour, 35*, 387-394.

Glander, K.E., Tapia, R.J., & Fachin, T.A. (1984). The impact of cropping on wild populations of *Saguinus mystax* and *Saguinus fuscicollis* in Peru. *American Journal of Primatology, 7*, 89-97.

Glaston, A.R., Geilvoet-Soeteman, E., Hora-Pecek, E., & van Hoof, J.A.R.A.M. (1984). The influence of the zoo environment on the soical behaviour of groups of cotton-topped tamarins, *Saguinus oedipus oedipus. Zoo Biology, 3*, 241-253.

Goldizen, A.W. (1987a). Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behavioural Ecology and Sociobiology, 20*, 99-109.

Goldizen, A.W. (1987b). Tamarins and marmosets: Communal care of offspring. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate Societies* (pp. 34-43). Chicago: University of Chicago Press.

Goldizen, A.W. (1988). Tamarin and marmoset mating systems: Unusual flexibility. *Trends in Ecology and Evolution, 3*, 36-40.

Goldizen, A.W. (1989). Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). *Behavioural Ecology and Sociobiology, 24*, 79-89.

Goldizen, A.W. (1990). A comparative perspective on the evolution of tamarin and marmoset social systems. *International Journal of Primatology, 11*, 63-83.

Goldizen, A.W., & Terborgh, J. (1986). Cooperative polyandry and helping behaviour in saddle-backed tamarins (*S. fuscicollis*). In J.G. Else & P.C. Lee (Eds.), *Primate Ecology and Conservation* (pp. 191-198). Cambridge: Cambridge University Press.

Goldizen, A.W., & Terborgh, J. (1989). Demography and dispersal patterns of a tamarin population: possible causes of delayed breeding. *American Naturalist, 134*, 208-224.

Goldizen, A.W., Terborgh, J., Cornejo, F., Porras, D.T., & Evans, R. (1988). Seasonal food shortage, weight loss, and the timing of births in saddle-back tamarins (*Saguinus fuscicollis*). *Journal of Animal Ecology, 57*, 893-901.

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of behavior.* Cambridge, Massachusetts: Belknap Press.

Goodall, J. (1973). Cultural elements in a chimpanzee community. In W. Montagna (Ed.), *Precultural Primate Behavior: Symposium of the Fourth International Congress of Primatology* (pp. 144-184). Basel: Karger.

Gosling, L.M. (1980). Defence guilds of savannah ungulates as a context for scent communication. *Symposia of the Zoological Society of London, 45*, 195-212.

Goss-Custard, J.D. (1970). The responses of red shank (Tringa totanus) to spatial variations in the density of their prey. *Journal of Animal Ecology, 39*, 91-114.

Gould, S.J., & Lewontin, R.C. (1979). The Spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London, B, 205*, 581-598.

Graves, G.R., & Gotelli, N.J. (1993). Assembly of avian mixed-species flocks in Amazonia. *Proceedings of the National Academy of Sciences, U.S.A., 90*, 1388-1391.

Grether, G.F., Palombit, R.A., & Rodman, P.S. (1992). Gibbon foraging decisions and the marginal value model. *International Journal of Primatology, 13*, 1-17.

Hall, K.R.L. (1963). Observational learning in monkeys and apes. *British Journal of Psychology, 54*, 201-226.

Hamilton, W.D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology, 7*, 1-52.

Hamilton, W.D. (1971). Geometry of the selfish herd. *Journal of Theoretical Biology, 31*, 295-311.

Hamilton, W.D., Buskirk, R.E., & Buskirk, W.H. (1976). Defence of space and resources by chacma (*Papio ursinus*). *American Naturalist, 112*, 911-924.

Hardie, S.M. (1995). *The behaviour of mixed-species tamarin groups (*Saguinus labiatus *and* Saguinus fuscicollis*)*. Unpublished Ph.D. thesis, University of Stirling, Stirling.

Hardie, S.M. (1997). Exhibiting mixed-species groups of sympatric tamarins (*Saguinus* spp.) at Belfast Zoo. *International Zoo Yearbook, 35*, 261-266.

Hardie, S.M. (1998). Mixed-species tamarin groups (*Saguinus fuscicollis* and *Saguinus labiatus*) in northern Bolivia. *Primate Report, 50*, 39-62.

Hardie, S.M., & Buchanan-Smith, H.M. (1997). Vigilance in single- and mixed-species groups of tamarins (*S. labiatus* and *S. fuscicollis*). *International Journal of Primatology, 18*, 219-232.

Hardie, S.M., Day, R.T., & Buchanan-Smith, H. (1993). Mixed-species *Saguinus* groups at Belfast Zoological Gardens. *Neotropical Primates, 1*, 19-21.

Harding, R.S.O. (1981). An order of omnivores: nonhuman primate diets in the wild. In R.S.O. Harding & G. Teleki (Eds.), *Omnivorous Primates: Gathering and hunting in human evolution* (pp. 191-214). New York: Columbia University Press.

Harvey, P.H., & Clutton-Brock, T.H. (1981). Primate home-range size and metabolic needs. *Behavioural Ecology and Sociobiology, 8*, 151-155.

Hauser, M.D. (1988). Invention and social transmission: new data from wild vervet monkeys. In R. Byrne & A. Whiten (Eds.), *Machiavellian Intelligence* (pp. 327-343). Oxford: Clarendon Press.

Heinrich, B. (1979). *Bumblebee Economics*. Cambridge, Massachusetts: Harvard University Press

Heltne, P.G., Freese, C.H., & Whitesides, G. (1976). *Field survey of nonhuman primates in Bolivia.* Unpublished report, Pan American Health Organization (PAHO), Washington, D.C.

Hernández-Camacho, J., & Cooper, R.W. (1976). The nonhuman primates of Colombia. In R.W. Thorington Jr. & P.G. Heltne (Eds.) *Neotropical Primates: Field Studies and conservation* (pp. 35-69). Washington D.C.: National Academy of Sciences.

Hershkovitz, P. (1977). *Living New World Monkeys (Platyrrhini), Vol 1.* Chicago: University of Chicago Press.

Hershkovitz, P. (1979). Races of the emperor tamarin, *Saguinus imperator* Goeldi (Callitrichidae, Primates). *Primates, 20*, 277-287.

Hershkovitz, P. (1982). Subspecies and geographic distribution of black-mantled tamarins *Saguinus nigricollis* Spix (Primates Callitrichidae). *Proceedings of the Biological Society of Washington*, 95, 647-656.

Heyes, C.M. (1993). Imitation, culture and cognition. *Animal Behaviour, 46*, 999-1000.

Heyes, C.M. (1994). Social learning in animals: categories and mechanisms. *Biological Review, 69*, 207-231.

Heymann, E.W. (1987). A field observation of predation on a moustached tamarin (*S. mystax*) by an anaconda. *International Journal of Primatology, 8*, 193-195.

Heymann, E.W. (1990a). Interspecific relations in a mixed-species troop of moustached tamarins, *Saguinus mystax*, and saddle-back tamarins, *Saguinus fuscicollis* (Primates: Callitrichidae), at the Río Blanco, Peruvian Amazonia. *American Journal of Primatology, 21*, 115-127.

Heymann, E.W. (1990b). Reactions of wild tamarins *Saguinus mystax* and *Saguinus fuscicollis* to avian predators. *International Journal of Primatology, 11*, 327-337.

Heymann, E.W. (1990c). Social behaviour and infant carrying in a group of moustached tamarins, *Saguinus mystax* (Primates: Platyrrhini: Callitrichidae). *Primates, 31*, 193-196.

Heymann, E.W. (1991). Field observations on the scent marking behaviour of moustached tamarins, *Saguinus mystax* (Primates: Platyrrhini), in north-eastern Peru. *Abstracts - Symposium on Chemical Signals in Vertebrates VI, Philadelphia*, 67.

Heymann, E.W. (1995). Sleeping habits of tamarins, *S. mystax* and *S. fuscicollis* (Mammalia; Primates; Callitrichidae), in north-eastern Peru. *Journal of Zoology, London, 237*, 211-226.

Heymann, E.W. (1996). Social behavior of wild moustached tamarins, *Saguinus mystax*, at the Estación Biológica Quebrada Blanco, Peruvian Amazonia. *American Journal of Primatology, 38*, 101-113.

Heymann, E.W. (1997). The relationship between body-size and mixed-species troops of tamarins (*Saguinus* spp.). *Folia Primatologica, 68*, 287-296.

Heymann, E.W., & Sicchar-Valdez, L.A. (1988). Interspecific social grooming in a mixed troop of tamarins, *S. mystax* and *S. fuscicollis* (Platyrrhini: Callitrichidae), in an outdoor enclosure. *Folia Primatologica, 50*, 221-225.

Heymann, E.W., & Buchanan-Smith, H.M. (submitted). The behavioural ecology of mixed-species troops of callitrichine primates. *Biological Reviews of the Cambridge Philosophical Society.*

Heymann, E.W., Sicchar-Valdez, L.A., & Tapia, R.J. (1996). Experiences with mixed-species housing of tamarins, *S. fuscicollis* and *S. mystax* (Primates: Callitrichidae), in an outdoor enclosure. *Zoologischer Garten NF, 66*, 381-390.

Hikami, K. (1991). Social transmission of learning in Japanese monkeys (*Macaca fuscata*). In A. Ehara, T. Kimura, O. Takenaka, M. Iwamoto (Eds.) *Primatology Today* (pp. 343-344). Amsterdam: Elsevier.

Hikami, K., Hasegawa, Y., Matsuzawa, T. (1990). Social transmission of food preferences in Japanese monkeys (*Macaca fuscata*) after mere exposure of aversion learning. *Journal of Comparative Psychology, 104*, 233-237.

Hill, R.A., & Lee, P.C. (1998). Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *Journal of Zoology, London, 245*, 447-456.

Hinde, R.A. (1973). On the design of check-sheets. *Primates, 14*, 393-406.

Hladik, A., & Hladik, C.M. (1969). Rapports trophiques entre végétation et primates dans le forêt de Barro Colorado (Panama). *Terre et la Vie, 1*, 25-117.

Hladik, C.M. (1977). Chimpanzees of Gabon and chimpanzees of Gombe: Some comparative data on the diet. In T.H. Clutton-Brock (Ed.), *Primate Ecology: Studies in feeding and ranging behaviour in lemurs, monkeys and apes* (pp. 481-501). London: Academic Press.

Ho, L.C. (1992). Fruit growth and sink strength. In C. Marshall & J. Grace (Eds.), *Fruit and seed production: Aspects of development, environmental physiology and ecology* (pp. 101-124). Cambridge: Cambridge University Press.

Hodge, M.A., & Uetz, G.W. (1992). Antipredator benefits of single-species and mixed-species grouping by *Nephila claviceps* (L.), (Araneae, Tetragnathidae). *Journal of Arachnology, 209*, 212-216.

Hodge, M.A., & Uetz, G.W. (1996). Foraging advantages of mixed-species association between soiltary and colonial orb-weaving spiders. *Oecologia, 107*, 578-587.

Holenweg, A.-K., Noë, R., & Schabel, M. (1996). Waser's gas model applied to a associations between red colobus and Diana monkeys in the Tai National Park, Ivory Coast. *Folia Primatologica, 67,* 125-136.

Hubbell, S.P. (1979). Tree dispersion, abundance and diversity in a tropical dry forest. *Science, 203,* 1299-1309.

Hubrecht, R.C. (1984). Field observations on group size and composition of the common marmoset (*Callithrix jacchus jacchus*), at Tapacurá, Brazil. *Primates, 25,* 13-21.

Hubrecht, R.C. (1985). Home-range size and use and territorial behaviour in the common marmoset, *Callithrix jacchus jacchus,* at the Tapacura Field Station, Recife, Brazil. *International Journal of Primatology, 6,* 533-550.

Hughes, R.N. (1979). Optimal diets under the energy maximization premise: the effects of recognition time and learning. *American Naturalist, 113,* 209-221.

Itani, J., & Nishimura, A. (1973). The study of infra-human culture in Japan. In W. Montagna (Ed.), *Precultural Primate Behavior: Symposium of the Fourth International Congress of Primatology* (pp. 26-50). Basel: Karger.

Itzkovitz, M. (1977). Social dynamics of mixed-species groups of Jamaican reef fishes. *Behavioural Ecology and Sociobiology, 2,* 361-384.

Iwasa, Y., Higashi, M., & Yamamura, N. (1981). Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist, 117,* 710-723.

Izawa, K. (1975). Foods and feeding behaviour of monkeys in the upper Amazon basin. *Primates, 16,* 295-316.

Izawa, K. (1978). A field study of the ecology and behaviour of the black-mantled tamarin *Saguinus nigricollis*. *Primates, 19,* 241-274.

Izawa, K. (1979). Food and feeding behaviour in wild black-capped capuchin (*Cebus apella*). *Primates, 21*, 57-76.

Izawa, K., & Bejarano, G. (1981). *Distribution ranges and patterns of nonhuman primates in western Pando, Bolivia.* Kyoto University Overseas Research Reports of New World Monkeys, II, 1-13.

Izawa, K., & Yoneda, M. (1981). *Habitat utilization of nonhuman primates in a forest of western Pando, Bolivia.* Kyoto University Overseas Research Reports of New World Monkeys, II, 13-22.

Jacobs, G.H. (1981). *Comparative Color Vision.* New York: Academic Press.

Jacobs, G.H. (1993). The distribution and nature of colour vision among the mammals. *Biological Reviews, 68*, 413-471.

Jacobs, G.H., Neitz, J., & Crognate, M. (1987). Colour vision polymorphism and its photopigment basis in a callitrichid monkey (*Saguinus fuscicollis*). *Vision Research, 27*, 2089-2100.

Jacobs, G.H., Neitz, M., Deegan, J.F., & Neitz, J. (1996). Trichromatic colour vision in New World monkeys. *Nature, 382*, 156-158.

Janson, C.H. (1983). Foraging for prey. In J. Terborgh (Ed.) *Five New World Primates: A study in comparative ecology* (pp. 96-128). Princeton, New Jersey: Princeton University Press.

Janson, C.H. (1988). Food competition in brown capuchin monkeys (*Cebus apella*): quantitative effects of group size and tree productivity. *Behaviour, 105*, 53-76.

Janson, C.H., & Goldsmith, M.L. (1995). Predicting group size in primates: foraging costs and predation risks. *Behavioural Ecology, 6*, 326-336.

Janson, C.H., & van Schaik, C.P. (1988). Recognizing the many faces of primate food competition: Methods. *Behaviour, 105*, 165-186.

Janson, C.H., Terborgh, J., & Emmons, L.H. (1981). Non-flying mammals as pollinating agents in the Amazonian forest. *Biotropica* (*Suppl.*), *14*, 1-6.

Janzen, D.H. (1973). Sweep samples of tropical foliage insects: description of study sites, with data on species abundances and size distributions. *Ecology, 54*, 659-686.

Jarvik, M.E. (1953). Discrimination of colored food and food signs by primates. *Journal of Comparative and Physiological Psychology, 46*, 390-392.

Jouventin, P., Pasteur, G., & Cambefort, J.P. (1976). Observational learning of baboons and avoidance of mimics. Exploratory tests. *Evolution, 31*, 21-28.

Julliot, C. (1996). Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. *American Journal of Primatology, 40*, 261-282.

Kagel, J.H., Green, L., & Caraco, T. (1986). When foragers discount the future: constraint or adaptation? *Animal Behaviour, 34*, 271-283.

Kamil, A.C. (1978). Systematic foraging by a nectar-feeding bird, the Amakihi (*Loxops vivens*). *Journal of Comparative and Physiological Psychology, 92*, 388-396.

Kamil, A.C. (1984). Adaptation and cognition; Knowning what comes naturally. In H. Roitblat, T.G. Bever, & H.S. Terrace (Eds.), *Animal Cognition* (pp. 533-544). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Kamil, A.C., & Yoerg, S.I. (1982). Learning and foraging behavior. In P.P.G. Bateson & P.H. Klopfer (Eds.), *Perspectives in Ethology* (pp. 325-364). New York: Plenum Press.

Kawamura, S. (1959). The process of sub-culture propagation among Japanese macaques. *Primates, 2*, 43-60.

Keddy, P.A. (1989). *Competition*. London: Chapman & Hall.

Kiltie, R. (1981). Application of search theory to the analysis of prey aggregation as an antipredation tactic. *Journal of Theoretical Biology, 87*, 201-206.

Kinzey, W.G. (1977). Diet and feeding behaviour of *Callicebus torquatus*. In T.H. Clutton-Brock (Ed.), *Primate Ecology: Studies in feeding and ranging behaviour in lemurs, monkeys and apes* (pp. 127-151). London: Academic Press.

Kinzey, W.G. (1997). *New World Primates: Ecology, evolution and behavior*. New York: Aldine de Gruyter.

Kinzey, W.G., Rosenberger, A.L., & Ramirez, M. (1975). Vetical, clinging and leaping in a neotropical anthropoid. *Nature, 225*, 327-328.

Kirkwood, J.K., & Underwood, S.J. (1984). Energy requirements of captive cotton-top tamarins (*Saguinus oedipus oedipus*). *Folia Primatologica, 42*, 180-187.

Kleiman, D.G. (1977). Monogamy in mammals. *Quarterly Review of Biology, 52*, 36-69.

Klein, L.L., & Klein, D.J. (1973). Observations of two types of Neotropical primate intertaxa associations. *American Journal of Physical Anthropology, 38*, 649-654.

Knogge, C., Heymann, E.W., Emerita, R., & Herrera, T. (1998). Seed dispersal of *Asplundia peruviana* (Cyclanthaceae) by the primate *Saguinus fuscicollis*. *Journal of Tropical Ecology, 14*, 99-102.

Koenig, A. (1995). Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology, 35*, 311-317.

Kohlhaas, A.K. (1991). Primate populations in northern Bolivia. *Primate Conservation, 9*, 93-97.

Krebs, J.R. (1973). Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). *Canadian Journal of Zoology, 51*, 1275-1288.

Krebs, J.R., & McCleery, R.H. (1984). Optimization in behavioural ecology. In J.R. Krebs & N.B. Davies (Eds.), *Behavioural Ecology: An evolutionary approach* (pp. 91-121). Sunderland, Massachusetts: Sinauer Assoc. Inc.

Krebs, J.R., MacRoberts, M.H., & Cullen, J.M. (1972). Flocking and feeding in the great tit *Parus major* - an experimental study. *Ibis, 114*, 507-530.

Krebs, J.R., Ryan, J., & Charnov, E.L. (1974). Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Animal Behaviour, 22*, 953-964.

Krebs, J.R., Kacelnik, A., & Taylor, P. (1978). Tests of optimal sampling by foraging great tits. *Nature, 275*, 27-31.

Kummer, H. (1971). *Primate Societies: Group techniques of ecological adaptation.* Chicago: University of Chicago Press.

Lacher, T.E., Jr., Fonseca, G.A.B. da, Alves, C., Jr., & Magalhães-Castro, B. (1981). Exudate-eating, scent-marking and territoriality in a wild population of marmosets. *Animal Behaviour, 29*, 306-307.

Lachlan, R.F., Crooks, L., & Laland, K.N. (1998). Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour, 56*, 181-190.

Lack, D. (1968). *Ecological Adaptations for Breeding in Birds.* London: Methuen.

Laland, K.N., & Plotkin, H.C. (1990). Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). *Animal Learning and Behaviour, 18*, 246-251.

Laland, K.N., & Williams, K. (1997). Shoaling generates social learning of foraging information in guppies. *Animal Behaviour, 53*, 1161-1169.

Laland, K.N., & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioural Ecology, 9*, 493-499.

Laland, K.N., Richerson, P.J. & Boyd, R. (1993). Animal social learning: towards a new theoretical approach. In P.P.G. Bateson, P.H. Klopfer & N.S. Thompson (Eds.), *Perspectives in Ethology, Vol. 10* (pp. 249-277). New York: Plenum Press.

Laland. K.N., Richerson, P.J., & Boyd, R. (1996). Developing a theory of animal social learning. In C.M. Heyes & B.G. Galef, Jr. (Eds.), *Social Learning in Animals: The roots of culture* (pp. 129-154). New York: Academic Press.

Landeau, J., & Terborgh, J. (1986). Oddity and the 'confusion effect' in predation. *Animal Behaviour, 34*, 1372-1380.

Latta, S.C., & Wunderle, J.M. (1996). The composition and foraging ecology of mixed-species flocks in pine forests of Hispaniola. *Condor, 98*, 595-607.

Lea, S.E.G. (1979). Foraging and reinforcement schedules in the pigeon: Optimal and non-optimal aspects of choice. *Animal Behaviour, 27*, 875-886.

Lea, S.E.G. (1981). Correlation and contiguity in foraging behaviour. In Z. Harem & M.D. Zeiler (Eds.), *Predictability, Correlation, and Contiguity*. London: John Wiley & Sons.

Lefebvre, L., & Giraldeau, L-A. (1996). Is social learning an adaptive specialization? In C.M. Heyes & B.G. Galef, Jr. (Eds.), *Social Learning in Animals: The roots of culture* (pp. 107-128). London: Academic Press.

Lefebvre, L., Palameta, B., & Hatch, K.K. (1996). Is group living associated with social learning? A comparative test of a gregarious and a territorial columbid. *Behaviour, 133*, 241-161.

Leigh, E.G., Jr., & Smythe, N. (1978). Leaf production, leaf consumption, and the regulation of folivory on Barro Colorado Island. In G.G. Montgomery (Ed.), *The Ecology of Arboreal Folivores* (pp. 51-73). Washington, D.C.: Smithsonian Institution Press.

Lepoivre, H., & Pallaud, B. (1985). Social facilitation in a troop of Guinea baboons (*Papio papio*) living in an enclosure. *Behavioural Processes, 11*, 405-418.

Lepoivre, H., & Pallaud, B. (1986). Learning set formation in a group of Guinea baboons (*Papio papio*): Importance of the behavioural variable measured. *American Journal of Primatology, 10*, 25-36.

Leutenegger, W. (1973). Maternal-fetal weight relationships in primates. *Folia Primatologia, 20*, 280-293.

Leutenegger, W. (1979). Evolution of litter-size in primates. *American Naturalist, 114*, 525-531.

Leutenegger, W. (1980). Monogamy in callitrichids: a consequence of phyletic dwarfism. *International Journal of Primatology, 1*, 95-98.

Leuthold, W. (1977). *African Ungulates: A comparative review of their ethology and behavioural ecology.* New York: Springer-Verlag.

Levine, M. (1959). A model of hypothesis behavior in discrimination learning set. *Psychological Review, 66*, 353-366.

Lindsay, N.B.D. (1979). A report on the field study of Geoffroy's tamarin *Saguinus oedipus geoffroyi. Dodo, Journal of the Jersey Wildlife Preservation Trust, 16*, 27-51.

Lopes, M.A., & Ferrari, S.F. (1994). Foraging behaviour of tamarin group (*Saguinus fuscicollis weddelli*) and interactions with marmosets (*Callithrix emiliae*). *International Journal of Primatology, 15*, 373-387.

Lorenz, K. (1960). Methods of approach to the problems of behaviour. *The Harvey Lectures, 1958-59* (pp. 60-103). New York: Academic Press.

MacDonald, S.E., Pang, J.C., & Gibeault, S. (1995). Marmoset (*Callithrix jacchus jacchus*) spatial memory in a foraging task - Win-stay versus win-shift strategies. *Journal of Comparative Psychology, 108*, 328-334.

MacKinnon, J.R., & MacKinnon, K.S. (1980). Niche differentiation in a primate community. In D. Chivers (Ed.), *Malayan Forest Primates: Ten years' study in tropical rain forest* (pp. 167-190). New York: Plenum Press.

Mahon, T.E, Kaiser, G.W., & Burger, A.E. (1992). The role of marbled marrelets in mixed-species feeding flocks in British Columbia. *Wilson Bulletin, 104*, 783-743.

Manning, A., & Dawkins, M.S. (1992). *An Introduction to Animal Behaviour.* Cambridge: Cambridge University Press.

Martin, P., & Bateson, P. (1986). *Measuring Behaviour.* Cambridge: Cambridge University Press.

Martins, E., Schneider, H., & Leão, V.F. (1987). Syntopy and troops association between *Callithrix* and *Saguinus* from Rondônia, Brazil. *International Journal of Primatology, 8*, 527. (Abstract).

Masataka, N. (1987). The perception of sex-specificity in long calls of the tamarin (*Saguinus labiatus*). *Ethology, 76*, 56-64.

May, R.M. (1973). *Stability and Complexity in Model Ecosystems. Monographs in Population Biology, Vol. 6.* Princeton: Princeton University Press.

Mayer, K.E., Blum, C.A, & Caine, N.G. (1992). Comparative foraging styles of tamarins and squirrel monkeys. *American Journal of Primatology, 27*, 46. (Abstract).

Maynard Smith, J. (1978). Optimization theory in evolution. *Annual Review of Ecology and Systematics, 9,* 31-56.

Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

McGrew, W.C., & McLuckie, E.C. (1986). Philopatry and dispersion in the cotton-top tamarin, *Saguinus oedipus oedipus*: an attempted laboratory simulation. *International Journal of Primatology, 7*, 401-422.

McKenna, J.J. (1981). Primate infant caregiving behavior: Origins, consequences, and variability with emphasis on the common indian langur monkey. In D.J. Gubernick & P.H. Klopfer (Eds.), *Parental Care in Mammals* (pp. 389- 411). New York: Plenum Press.

McNamara, J. (1982). Optimal patch use in a stochastic environment. *Theoretical Population Biology, 21*, 269-285.

McNamara, J., & Houston, A. (1980). The application of statistical decision theory to animal behaviour. *Journal of Theoretical Biology, 85*, 673-690.

McShane, P. (1995). *A mixed-species free-ranging group of tamarins (*Saguinus fuscicollis weddelli *and* Saguinus labiatus labiatus*) at Belfast Zoological Gardens.* Unpublished M.Sc. thesis, Queens University of Belfast, Belfast.

Menzel, C.R., & Menzel, E.W. (1980). Head-cocking and visual exploration in marmosets, *Saguinus fuscicollis*. *Behaviour, 75*, 219-234.

Menzel, E.W., Jr. (1969). Responsiveness to food and signs of food in chimpanzee discrimination learning. *Journal of Comparative and Physiological Psychology, 68*, 484-489.

Menzel, E.W., Jr. (1973). Leadership and communication in young chimpanzees. In E.W. Menzel (Ed.), *Precultural Primate Behavior* (pp. 192-225). Basel: Karger.

Menzel, E.W. (1978). Cognitive mapping in chimpanzees. In S.H. Hulse, H. Fowler, & W.K. Honig (Eds.), *Cognitive Processes in Animal Behaviour* (pp. 375-422). New York: Academic Press.

Menzel, E.W. (1980). Head-cocking and visual perception in primates. *Animal Behaviour, 28*, 151-159.

Menzel, E.W. Jr., & Menzel, C.R. (1979). Cognitive, developmental and social aspects of responsiveness to novel objects in a family group of marmosets (*Saguinus fuscicollis*). *Behaviour, 70*, 251-277.

Menzel, E.W., & Juno, C. (1982). Marmosets (*Saguinus fuscicollis*): Are learning sets learned? *Science, 217*, 750-752.

Menzel, E.W., & Juno, C. (1984). Are learning sets learned? Or: Perhaps no nature-nurture issue has any simple answer. *Animal Learning and Behaviour, 12*, 111-115.

Menzel, E.W., & Juno, C. (1985). Social foraging in marmoset monkeys and the question of intelligence. *Philosophical Transactions of the Royal Society of London, B, 308*, 145-158.

Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *American Anthropologist, 83*, 534-548.

Milton, K. (1988). Foraging behaviour and the evolution of primate intelligence. In R.W. Byrne & A. Whiten (Eds.), *Machiavellian Intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans* (pp. 285-305). Oxford: Oxford University Press.

Mineka, S. & Cook, M. (1993). Social learning and the acquisition of snake fear in monkeys. In T. Zentall & B.G. Galef, Jr. (Eds.) *Social Learning: Psychological and biological perspectives* (pp. 51-73). Hillsdale, New Jersey: Lawrence Erlbaum.

Mitchell, W.A. (1989). Informational constraints on optimally foraging hummingbirds. *Oikos, 55*, 145-154.

Mittermeier, R.A. (1977). Distribution, synecology and conservtaion of Suriname monkeys. Unpublished Ph.D. thesis, Harvard University, Cambridge, Massachusetts.

Mittermeier, R.A., & Coimbra-Filho, A.F. (1981). Systematics: species and subspecies. In R.A. Mittermeier, A.B. Rylands, A. Coimbra-Filho, & G.A.B. Fonesca. (Eds.), *Ecology and Behavior of Neotropical Primates, Vol. 2* (pp. 223-298). Washington D.C: WWF.

Mittermeier, R.A., & Combra-Filho, A.F. (1977). Primate conservation in Brazilian Amazonia. In H.S.H. Prince Rainier III of Monaco & G.H. Bourne (Eds.), *Primate Conservation* (pp. 117-166). New York: Academic Press.

Mittermeier, R.A., & Roosmalen, M.G.M., van (1981). Preliminary observations on habitat utilization and diet in eight Surinam monkeys. *Folia Primatologica, 44*, 82-95.

Mittermeier, R.A., Rylands, A.B., & Coimbra-Filho, A.F. (1988). Systematics: Species and subspecies - an update. In R.A. Mittermeier, A.B. Rylands, A.F. Coimbra-Filho, & G.A.B. da Fonseca (Eds.), *Ecology and Behaviour of Neotropical Primates, Vol. 2* (pp. 13-75). Washington, D.C.: World Wildlife Fund.

Mollon, J.D. (1989). "Tho' she kneel'd in that place where they grew..." The uses and origins of primate colour vision. *Journal of Experimental Biology, 146*, 21-38.

Mollon, J.D. (1991). Uses and evolutionary origins of primate colour vision. In J.R. Cronly-Dillon & R.L. Gregory (Eds.), *Evolution of the Eye and Visual System* (pp. 306-391). Boca Raton: CRC Press.

Mollon, J.D., Bowmaker, J.K., & Jacobs, G.H. (1984). Variations of colour vision in a New World primate can be explained by polymorphism of retinal photopigments. *Proceedings of the Royal Society, London, B, 222*, 373-399.

Moody, M.F., & Menzel, E.W. (1976). Vocal communication in marmosets (*Saguinus fuscicollis*). *Folia Primatologica, 25*, 73-94.

Moore, K., Cleland. J., & McGrew, W.C. (1991). Visual encounters between families of cotton-top tamarins, *Saguinus (o.) oedipus*. *Primates, 32*, 23-33.

Morgan, C.L. (1900). *Animal Behaviour*. London: Edward Arnold.

Morgan, M.J., Adam, A., & Mollon, J.D. (1992). Dichromats detect color-camouflaged objects that are not detected by trichromats. *Proceedings of the Royal Society, London, B, 248*, 291-295.

Morse, D.H. (1970). Ecology aspect of some mixed-species foraging flocks of birds. *Ecological Monographs, 40*, 119-168.

Morse, D.H. (1980). *Behavioral Mechanisms in Ecology*. Cambridge, Massachusetts: Harvard Univeristy Press.

Moynihan, M. (1962). The organization and probable evolution of some mixed-species flocks of neotropical birds. *Smithsonian Miscellaneous Collections, 143*, 1-140.

Moynihan, M. (1970). Some behavior patterns of platyrrhine monkeys: II. *Saguinus geoffroyi* and some other tamarins. *Smithsonian Contributions to Zoology, 28*, 1-77.

Moynihan, M. (1976). *The New World primates*. Princeton, New Jersey: Princeton University Press.

Munn, C.A., & Terborgh, J.W. (1980). Multi-species territoriality in Neotropical foraging foraging flocks. *Condor, 81*, 338-347.

Napier, J.R., & Napier, P.H. (1967). *A Handbook of Living Primates*. New York: Academic Press.

Nash, L.T. (1986). Dietary, behavioural and morphological aspects of gummivory in primates. *Yearbook of Physical Anthroplogy, 29*, 113-137.

Neill, S.R., & Cullen, J.M. (1974). Experiments on whether schooling by their prey affects the hunting behvaiour of cephalopods and fish predators. *Journal of Zoology, London, 172*, 549-569.

Newton, I. (1967). The adaptive radiation and feeding ecology of some British finches. *Ibis, 109*, 33-94.

Neyman, P.F. (1978). Aspects of the ecology and social organisation of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In D.G. Kleiman (Ed.), *Biology and Conservation of the Callitrichidae* (pp, 39-71). Washington D.C.: Smithsonian Institution Press.

Neyman, P.F. (1980). *Ecology and social organization of cotton-top tamarin (*Saguinus oedipus). Unpublished Ph.D. thesis, University of California, Berkeley.

Nickle, D.A., & Heymann, E.W. (1996). Predation on Orthoptera and other orders of insects by tamarin monkeys, *Saguinus mystax mystax* and *Saguinus fuscicollis nigrifrons* (Primates: Callitrichidae), in north-eastern Peru. *Journal of Zoology, London, 239,* 799-819.

Nishida, T., Wrangham, R.W., Goodall, J., & Uehara, S. (1983). Local differnces in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania. *Journal of Human Evolution, 12,* 467-480.

Noldus (1993). *The Observer: System for collection and analysis of observational data.* Wageningen, Netherlands: Noldus Information Technology b.v.

Norconk, M.A. (1985). *Mixed species troops of* Saguinus mystax *and* S. fuscicollis*: Group dynamics.* Paper presented at the Annual Meeting of the American Association of Physical Anthropologists, Knoxville.

Norconk, M.A. (1986). *Interactions between primate species in a neotropical forest: mixed species troops of* Saguinus mystax *and* S. fuscicollis *(Callitrichidae).* Unpublished Ph.D. thesis, University of California, Los Angeles.

Norconk, M.A. (1990a). Introductory remarks: ecological and behavioral correlates of polyspecific primate troops. *American Journal of Primatology, 21,* 81-85.

Norconk, M.A. (1990b). Mechanisms promoting stability in mixed *Saguinus mystax* and *S. fuscicollis* troops. *American Journal of Primatology, 21,* 129-146.

O'Toole, C. (1995). *Alien Empire: An exporation of the lives of insects.* London: BBC Books.

Oaten, A. (1977). Optimal foraging in patches: a case for stochasticity. *Theoretical Population Biology, 12,* 263-285.

Oates, J.F. (1987). Food distribution and foraging behavior. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate Societies* (pp. 197-209). Chicago: University of Chicago Press.

Oates, J.F., & Whitesides, G.H. (1980). Association between olive colobus (*Procolobus verus*), Diana guenons (*Cercopithecus diana*), and other forest monkeys in Sierra Leone. *American Journal of Primatology, 21*, 129-146.

Ogden, J.D., & Wolfe, L.G. (1979). Reproduction of wild caught marmosets (*Saguinus labiatus labiatus*) under laboratory conditions. *Laboratory Animal Science, 29*, 545-546.

Olton, D.S. (1982). Staying and shifting: their effects on discrimination learning. In M.L. Commons, R.J. Herrnstein & H. Rachlin (Eds.), *Quantitative Analyses of Behavior, Vol. II: Matching and maximizing accounts* (pp. 205-225). Cambridge, Massachusetts: Ballinger Publishing Company.

Olton, D.S., Handelman, G.E., & Walker, J.A. (1981). Spatial Memory and Food Searching Strategies. In A.C. Kamil & T.D. Sargent (Eds.), *Foraging Behaviour: Ecological, Ethological, and Psychological Approaches* (pp. 333-354). New York: Garland Press.

Olupot, W., Waser, P.M., Chapman, C.A. (1998). Fruit feeding by mangabeys (*Lophocebus albigena*): are monitoring of fig trees and use of sympatric frugivore calls possible strategies? *International Journal of Primatology, 19*, 339-353.

Opler, P.A., Baker, H.G., & Frankie, G.W. (1980). Plant reproductive characteristics during secondary succession in neotropical lowland forest ecosystems. *Biotropica, 12 (Suppl.)*, 40-46.

Orians, G.H. (1981). Foraging behaviour and the evolution of discriminatory abilities. In A.C. Kamil & T.D. Sargent (Eds.), *Foraging behavior: Ecological, ethological, and psychological approaches* (pp. 389-408). New York: Garland STPM Press.

Osorio, D., & Vorobyev, M. (1996). Colour vision as an adaptation to frugivory in primates. *Proceedings of the Royal Society, London, B, 263*, 593-599.

Peres, C.A. (1986a). *Costs and benefits of territorial defense in the golden lion tamarin,* Leontopithecus rosalia. Unpublished Masters thesis, University of Florida, Gainesville.

Peres, C.A. (1986b). Golden lion tamarin project. II. Ranging patterns and habitat selection in golden lion tamarins *Leontopithecus rosalia* (Linnaeus, 1766) Callitrichidae, Primates. In M.T. de Mello (Ed.), *A primatologia no Brasil-2* (pp. 223-241). Brasília: Sociedade Brasileira de Primatologia.

Peres, C.A. (1989). Exudate-eating by wild golden lion tamarins, *Leontopithecus rosalia. Biotropica, 21*, 287-288.

Peres, C.A. (1991). *Ecology of mixed species groups of tamarins in Amazonian terra firme forests.* Unpublished Ph.D. thesis, University of Cambridge, Cambridge.

Peres, C.A. (1992a). Consequences of joint-territoriality in a mixed-species group of tamarin monkeys. *Behaviour, 123*, 220-246.

Peres, C.A. (1992b). Prey-capture benefits in a mixed-species group of Amazonian tamarins, *Saguinus fuscicollis* and *S. mystax. Behavioural Ecology and Sociobiology, 31*, 339-347.

Peres, C.A. (1993a) Anti-predator benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica, 61*, 61-76.

Peres, C.A. (1993b). Diet and feeding ecology of saddle-back (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins in an Amazonian *terra firme* forest. *Journal of Zoology, London, 230*, 567-592.

Peres, C.A. (1994). Primate responses to phenological changes in Amazonian terra firme forest. *Biotropica,* 26, 98-112.

Peres, C.A. (1996). Food patch structure and plant resource partitioning in interspecific associations of Amazonian tamarins. *International Journal of Primatology, 17*, 695-723.

Peres, C.A., Patton, J.L., & da Silva, M.N.F. (1996). Riverine barriers and gene flow in Amazonian saddle-back tamarins. *Folia Primatologica, 67*, 113-124.

Pianka, E.R. (1988). *Evolutionary Ecology*. New York: Harper & Row.

Pilleri, G., & Knuckley, J. (1969). Behaviour patterns of some Delphinidae observed in the western Mediterranean. *Zeitschrift für Tierpsychologie, 26*, 48-72.

Plotkin, H.C. (1988). Learning and evolution. In H.C. Plotkin (Ed.), *The Role of Behaviour in Evolution* (pp. 133-164). Cambridge: MIT Press.

Podolsky, R.D. (1990). Effects of mixed-species association on resource use by *Saimiri sciureus* and *Cebus appella*. *American Journal of Primatology, 21*, 147-158.

Polyak, S. (1957). *The vertebrate visual system*. Chicago: University of Chicago Press.

Pook, A.G., & Pook, G. (1981). A field study of the socioecology of the Goeldi's monkey (*Callimico goedlii*) in northern Bolivia. *Folia Primatologica, 35*, 288-312.

Pook, A.G., & Pook, G. (1982). Polyspecific association between *Saguinus fuscicollis*, *Saguinus labiatus*, *Callimico goeldii*, and other primates in north-western Bolivia. *Folia Primatologica, 38*, 196-216.

Post, D.G. (1984). Is optimization the optimal approach to primate foraging? In P.S. Rodman & J.G.H. Cant (Eds.), *Adaptations for Foraging in Nonhuman Primates* (pp. 280-303). New York: Columbia University Press.

Powell, G.V.N. (1989). On the possible contribution of mixed-species flocks to species richness in Neotropical avifaunas. *Behavioural Ecology and Sociobiology, 24*, 387-393.

Price, E.C. (1990a). Parturition and perinatal behaviour in captive cotton-top tamarins (*Saguinus odeipus*). *Primates, 31*, 523-535.

Price, E.C. (1990b). Infant-carrying as a courtship strategy of breeding male cotton-top tamarins. *Animal Behaviour, 40*, 784-786.

Price, E.C. (1992). The costs of infant carrying in captive cotton-top tamarins. *American Journal of Primatology, 26*, 23-33.

Price, E.C., & Feistner, A.T.C. (1993). Food sharing in lion tamarins - Tests of three hypotheses. *American Journal of Primatology, 31*, 211-221.

Price, E.C., McGivern, A.M., & Ashmore, L. (1991). Vigilance in a group of free-ranging cotton-top tamarins (*Saguinus oedipus*). *Dodo, Journal of the Jersey Wildlife Preservation Trust, 27*, 41-49.

Price, J.A. (1975). Sharing: The integration of intimate economies. *Anthropologica, 17*, 3-27.

Pruetz, J.D., & Garber, P.A. (1991). Patterns of resource utilization, home range overlap, and intergroup encounters in moustached tamarin monkeys. *American Journal of Physical Anthropology, Suppl. 12*, 146 (Abstract).

Pryce, C.R. (1988). Individual and group effects on early caregiver-infant relationships in red-bellied tamarin monkeys. *Animal Behaviour, 36*, 1455-1464.

Pulliam, H.R., & Millikan, G.C. (1982). Social organization in the nonreproductive season. In D.S. Farner, J.R. King & K.C. Parkes (Eds.) *Avian Biology, Vol. VI.* New York: Academic Press.

Pulliam, H.R., & Caraco, T. (1984). Living in groups: Is there an optimal group size? In J.R. Krebs & N.B. Davies (Eds.) *Behavioural Ecology: An evolutionary approach* (pp.122-147). Sunderland, Massachusetts: Sinauer Assoc. Inc.

Pyke, G.H. (1974). *Studies in the foraging efficiency of animals.* Ph.D. thesis, University of Chicago, Chicago.

Pyke, G.H. (1978). Optimal foraging in hummingbirds: testing the marginal value theorem. *American Zoologist, 18*, 739-752.

Pyke, G.H. (1981). Hummingbird foraging on artificial inflorescences. *Behaviour Analysis Letters, 1*, 11-15.

Pyke, G.H. (1984). Optimal Foraging Theory: A Critical Review. *Annual Review of Ecological Systematics, 15*, 523-575.

Pyke, G.H., Pulliam, H.R., & Charnov, E.L. (1977). Optimal foraging: A selective review of theory and tests. *Quarterly Review of Biology, 52*, 137-154.

Ramirez, M. (1984). Population recovery in the moustached tamarin (*Saguinus mystax*): management strategies and mechanisms. *American Journal of Primatology, 8*, 205-213.

Ramirez, M. (1989). *Feeding ecology and demography of the moustached tamarin,* Saguinus mystax, *in northeastern Peru.* Unpublished Ph.D. thesis, City University of New York, New York.

Ramirez, M., Freese, C., & Revilla, J. (1978). Feeding ecology of the pygmy marmoset, *Cebuella pygmaea*, in north-eastern Peru. In D.G. Kleiman (Ed.), *Biology and Conservation of the Callitrichidae* (pp. 23-27). Washington D.C.: Smithsonian Institution Press.

Real, L., Ott, J., & Silverfine, E. (1982). On the trade-off between the mean and the variance in foraging: Effect of spatial distribution and color preference. *Ecology, 63*, 1617-1623.

Redican, W.K. (1975). Facial expressions in non-human primates. In L.A. Rosenblum (Ed.), *Primate Behavior* (pp. 103-194). New York: Academic Press.

Regan, B.C., Viénot, F., Charles-Dominique, P.C., Pefferkorn, S., Simmen, B., Julliot, C., Mollon, J.D. (1996). The colour signals that fruits present to primates. *Investigative Opthalmology and Visual Science, 37*, 2997.

Richard, A.F. (1981). Changing assumptions in primate ecology. *American Anthropologist, 83*, 517-533.

Richard, A.F. (1985). *Primates in Nature.* New York: W.H. Freeman & Company.

Richards, P.W. (1952). *The Tropical Rain Forest.* Cambridge: Cambridge University Press.

Ricklefs, R.E. (1975). Seasonal occurrence of night flying insects on Barro Colorado Island. *Journal of the New York Entomological Society, 83*, 19-32.

Robinson, J.G. (1986). Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: Implications for foraging theory. *Smithsonian Contributions to Zoology, 431*, 1-60.

Robinson, M.H. (1969). The defensive behaviour of some orthopteroid insects from Panama. *Transactions of the Royal Entomological Society, London, 121*, 208-303.

Rogers, A.R. (1988). Does biology constrain culture? *American Anthroplogist, 90*, 819-831.

Rosenberger, A.L. (1977). *Xenothrix* and ceboid phylogeny. *Journal of Human Evolution, 6*, 461-481.

Rosenberger, A.L. (1981). Systematics: the higher taxa. In A.F. Coimbra-Filho & R.A. Mittermeier (Eds.) *Ecology and Behavior of Neotropical Primates* (pp. 9-27). Río de Janeiro: Academia Brasileira de Ciências.

Rothe, H., & Darms, K. (1993). The social organization marmosets: A critical evaluation of recent concepts. In A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology* (pp. 176-199). Oxford: Oxford University Press.

Rowell, T. (1979). How would we know if social organization were not adaptive? In I.S. Bernsetin & E.O. Smith (Eds.), *Primate Ecology and Human Origins: Ecological influences on social organization* (pp. 1-22). New York: Garland.

Royama, T. (1970). Factors governing the hunting behaviour and selection of food by the great tit (*Parus major* L.). *Journal of Animal Ecology, 39*, 619-668.

Rozin, P., & Kalat, J.W. (1971). Specific hungers and poison avoidance as adaptive specializations of learning. *Psychological Review, 78*, 459-486.

Rubenstein, D.I. (1978). On predation, competiton, and the advantages of group living. In P. Bateson & P. Klopfer (Eds.), *Perspectives in Ethology* (pp. 205-230). New York: Plenum Press.

Rubenstein, D.I., Barnett, R.J., Ridgley, R.S., & Klopfer, P.H. (1977). Adaptive advantages of mixed-species feeding flocks among seed-eating finches in Costa Rica. *Ibis, 119*, 10-21.

Rudran, R. (1978). Socioecology of the blue monkeys (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest, Uganda. *Smithsonian Contributions to Zoology, 249*, 1-88.

Ruiter, J.R., de (1986). The influence of group-size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (*Cebus olivaceus*). *Behaviour, 98*, 240-258.

Rumbaugh, D.M., Washburn, D., & Savage-Rumbaugh, S. (1989). On the care of captive chimpanzees: Methods of enrichment. In E.F. Segal (Ed.), *Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates* (pp. 357-375). Park Ridge, New Jersey: Noyes Publications.

Ruth, B. (1991). Social behavior of free-living tamarin monkeys (*Saguinus mystax*) on Padre Isla, Peru. *American Journal of Physical Anthropology Suppl. 12,* 156. (Abstract).

Rylands, A.B. (1981). Preliminary field observations on the marmoset, *Callithrix humeralifer intermedius* (Hershkovitz, 1977), at Dardanelos, Río Aripuanã, Mato Grosso. *Primates, 22*, 46-59.

Rylands, A.B. (1982). *The behaviour and ecology of three species of marmosets and tamarins (Callitrichidae, Primates) in Brazil.* Unpublished Ph.D. thesis, University of Cambridge, Cambridge.

Rylands, A.B. (1984). Exudate-eating and tree-gouging by marmosets (Callitrichidae, Primates). In A.C. Chadwick & S.L. Sutton (Eds.), *Tropical Rain Forest: The Leeds Symposium* (pp. 155-168). Leeds: Leeds Philosophical and Literary Society.

Rylands, A.B. (1985). Tree-gouging and scent-marking by marmosets. *Animal Behaviour, 33*, 1365-1367.

Rylands, A.B. (1986a). Infant-carrying in a wild marmoset group, *Callithrix humeralifer*: evidence for a polyandrous mating system. In M.T. de Mello (Ed.), *A primatologia no Brasil-2* (pp. 131-144). Brasília: Sociedade Brasileira de Primatologia.

Rylands, A.B. (1986b). The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkey (*Cebus olivaceus*). *Behaviour, 96*, 240-258.

Rylands, A.B. (1987). Primate communities in Amazonian forests: their habitats and food resources. *Experientia, 43*, 265-279.

Rylands, A.B. (1989). Sympatric Brazilian callitrichids: The black-tufted ear marmoset, *Callithrix kuhli*, and the golden-headed lion tamarin, *Leontopithecus chrysomelas*. *Journal of Human Evolution, 18*, 679-695.

Rylands, A.B. (1990). Scent marking behaviour of wild marmosets, *Callithrix humeralifer* (Callitrichidae, Primates). In D.W. MacDonald, D. Muller-Schwarze & S.E. Natynczuk (Eds). *Chemical Signals in Vertebrates 5* (pp. 415-429). Oxford: Oxford University Press.

Rylands, A.B. (1995). A species list for the New World primates (Platyrrhini): Distribution by country, endemism, and conservation status according to the Mace-Land System. *Neotropical Primates, 3 (Suppl.)*, 113-160.

Rylands, A.B. (1996). Habitat and the evolution of social and reproductive behaviour in Callitrichidae. *American Journal of Primatology, 38*, 5-18.

Rylands, A.B., Coimbra-Filho, A.F., & Mittermeier, R.A. (1993). Systematics, geographic distribution, and some notes on the conservation status of the Callitrichidae. In A.B. Rylands (Ed.), *Marmosets and Tamarins. Systematics, behaviour, and ecology* (pp. 11-77). Oxford: Oxford University Press.

Sakia, Y., & Kohda, M. (1995). Foraging by mixed-species groups involving a small angelfish *Centropyge ferrugatus* (Pomacanthidae). *Japansese Journal of Icthyology, 41*, 429-435.

Savage, A., Snowdon, C.T., Giraldo, H., & Rodriguez, J.V. (1989). *The ecology of the cotton-top tamarin (*Saguinus o. oedipus*) in Colombia - Progress Report, October, 1989.* In R. Colley (Ed.), British Is. & Ireland: Regional Studbook Cotton-topped Tamarin (*Saguinus o. oedipus*), No. 4 (1989).

Schaffer, W.M. (1978). A note on the theory of reciprocal altruism. *American Naturalist, 112*, 250-253.

Schneider, H., Schneider, M.P.C., Sampaio, I., Harada, M.L., Stanhope, M., Czelusinak, J., & Goodman, M. (1993). Molecular phylogeny of the New World monkeys (Platyrrhini, Primates). *Molecular Phylogenetics and Evolution, 2*, 225-242.

Schoener, T.W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics, 2*, 369-404.

Schoener, T.W. (1988). Ecological interactions. In A.A. Myers & P.S. Giller (Eds.), *Analytical Biogeography* (pp. 255-297). London: Chapman & Hall.

Sherman, P.W. (1977). Nepotism and the evolution of alarm calls. *Science, 197*, 1246-1253.

Sinclair, A.R.E. (1985). Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology, 54*, 899-918.

Skorupa, J.P., 1983. Monkeys and matrices: a second look. *Oecologia, 57*, 391-396.

Smith, A.C. (1997). *Comparative ecology of the saddleback (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*) tamarins*. Unpublished Ph.D. thesis, University of Reading, Reading.

Smith, J.N.M., & Dawkins, R. (1971). The hunting behaviour of individual great tits in relation to spatial variation in their food density. *Animal Behaviour, 19*, 695-706.

Smith, J.N.M., & Sweatman, H.P.A. (1974). Food-searching of titmice in patchy environments. *Ecology, 55*, 1216-1232.

Smythe, N. (1974). Biological monitoring data: Insects. In R.W. Rubinoff & T.L. Erwin (Eds.), *Environmental Monitoring and Baseline Data* (pp. 70-115). Washington, D.C.: Smithsonian Institution Environmental Science Program.

Snowdon, C.T., & Soini, P. (1988). The tamarins, genus *Saguinus*. In R.A. Mittermeier, A.B. Rylands, A. Coimbra-Filho, & G.A.B. de Fonesca. (Eds.), *Ecology and Behavior of Neotropical Primates, Vol. 2* (pp. 223-298). Washington D.C.: WWF.

Snowdon, C.T., Cleveland, J., & French, J.A. (1983). Responses to context-specific and individual-specific cues in cotton-top tamarin long calls. *Animal Behaviour, 31*, 92-101.

Snowdon, C.T., Ziegler, T.E., & Widowski, T.M. (1993). Further hormonal suppression of eldest daughter cotton-top tamarins following birth of infants. *American Journal of Primatology, 31*, 11-21.

Soini, P. (1982). Ecology and population dynamics of the pygmy marmoset, *Cebuella pygmaea*. *Folia Primatologica, 39*, 1-21.

Soini, P. (1987). Ecology of the saddle-back tamarin, *Saguinus fuscicollis illigeri* on the Río Pacaya, northeastern Peru. *Folia Primatologica, 49*, 11-32.

Soini, P. (1988). The pygmy marmoset, genus *Cebuella*. In R.A. Mittermeier, A.B. Rylands, A. Coimbra-Filho, & G.A.B. da Fonesca. (Eds.), *Ecology and Behavior of Neotropical Primates, Vol. 2* (pp. 79-129). Washington D.C.: World Wildlife Fund.

Soini, P. (1993). The ecology of the pygmy marmoset, *Cebuella pygmaea*: some comparisons with two sympatric tamarins. In A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology* (pp. 257-261). Oxford: Oxford University Press.

Soini, P., & Cóppula, M. (1981). Ecología y dinamica poblacional del pichico, *Saguinus fuscicollis* (Primates, Callitrichidae). Informe de Pacaya, No. 6. Ordeloreto, Dirección Regional de Agricultura y Alimentación, Iquitos, Peru.

Soini, P., & Soini, M., (1983). Distribución geográfica y ecologiá poblacional de *Saguinus mystax* (Primates, Callitrichidae). Informe de Pacaya, No. 6. Ordeloreto, Dirección Regional de Agricultura y Alimentación, Iquitos, Peru.

Spence, K.W. (1937). Experimental studies of learning and higher mental processes in infra-human primates. *Psychological Bulletin, 34*, 806-850.

Stacey, P. (1986). Group size and foraging efficiency in yellow baboons. *Behavioural Ecology and Sociobiology, 18*, 175-187.

Staddon, J.E.R. (1980). Optimality analyses of operant behaviour and their relation to optimal foraging. In J.E.R Staddon (Ed.), *Limits to Action: The allocation of Individual Behaviour*. New York: Academic Press.

Stafford, B.J., & Ferreira, F.M. (1995). Predation attempts on callitrichids in the Atlantic coastal rain forest of Brazil. *Folia Primatologica, 65*, 229-233.

Stephens, D.W., & Charnov, E.L. (1982). Optimal foraging: some simple stochastic models. *Behavioural Ecology and Sociobiology, 10*, 251-263.

Stevenson, M.F. & Rylands, A.B. (1988). The marmosets, genus *Callithrix*. In R.A. Mittermeier, A.B. Rylands, A.F. Coimbra-Filho, & G.A.B. da Fonesca (Eds.), *Ecology and Behaviour of Neotropical Primates* (pp. 131-222). Washington D.C.: World Wildlife Fund.

Steward, J.M. & Cole, B.L. (1989). What do colour-vision defectives say about everyday tasks. *Optometry and Vision Science, 66*, 288-295.

Stolz, L.P, & Saayman, G.S. (1970). Ecology and behaviour of baboons in the northern Transvaal. *Annals of the Transvaal Museum, 26*, 99-143.

Struhsaker, T.T. (1975). *The Red Colobus Monkey.* Chicago: University of Chicago Press.

Struhsaker, T.T. (1978). Food habits of five monkey species in the Kibale Forest, Uganda. In D.J. Chivers & J. Herbert (Eds.), *Recent Advances in Primatology, Vol. 1* (pp. 225-248). New York: Academic Press.

Struhsaker, T.T. (1981). Polyspecific associations among tropical rain-forest primates. *Zeitschrift für Tierpsychologie, 57*, 268-304.

Struhsaker, T.T., & Oates, J.F. (1979). Comparison of the behaviour and ecology of red colobus and black-and-white colobus monkeys in Uganda: A summary. In R.W. Sussman (Ed.), *Primate Ecology: Problem-orientated field studies* (pp. 165-183). New York: Wiley.

Sussman, R.W., & Garber, P.A. (1985). Communal breeding among the Callitrichidae and its adaptive significance. *American Journal of Physical Anthropology, 66*, 236.

Sussman, R.W., & Garber, P.A. (1987). A new intepretation of the social organization and mating system of the Callitrichidae. *International Journal of Primatology, 8*, 73-92.

Sussman, R.W., & Kinzey, W.G. (1984). The ecological role of the Callitrichidae. *Amerian Journal of Physical Anthropology, 64*, 419-449.

Symington, M.M. (1988). Food competition and foraging party size in the black spider monkey *Ateles paniscus chamek. Behaviour, 105*, 117-134.

Szalay, F.S., & Delson, E. (1979). *Evolutionary History of the Primates*. New York: Academic Press.

Tardif, S.D. (1994). Relative cost of infant care in small-bodied neotropical primates and its relation to infant care patterns. *American Journal of Primatology, 6*, 337-380.

Tardif, S.D., Richter, C.B., Carson, R.L. (1984). Effects of sibling-rearing experience on future reproductive success in two species of Callitrichidae. *American Journal of Primatology, 6*, 377-380.

Tardif, S.D., Harrison, M.L., & Simek, M.A. (1993). Communal infant care in marmosets and tamarins: relation to energetics, ecology, and social organization. In A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology* (pp. 220-234). Oxford: Oxford University Press.

Terborgh, J. (1983). *Five New World Primates: A study in comparative ecology*. Princeton, New Jersey: Princeton University Press.

Terborgh, J. (1985). The ecology of Amazonian primates. In G.T. Prance & T.E. Lovejoy (Eds.), *Amazonia* (pp. 284-304). New York: Pergamon Press.

Terborgh, J. (1986). The social systems of New World primates; an adaptionist view. In J J.G. Else & P.C. Lee (Eds.), *Primate Ecology and Conservation* (pp. 199-211). Cambridge: Cambridge University Press.

Terborgh, J. (1990). Mixed flocks and polyspecific associations: Costs and benefits of mixed groups to birds and monkeys. *American Journal of Primatology, 21*, 87-100.

Terborgh, J., & Goldizen, A.W. (1985). On the mating system of the cooperatively breeding saddle-back tamarin (*Saguinus fuscicollis*). *Behavioural Ecology and Sociobiology, 16*, 293-299.

Terborgh, J., & Janson, C. (1986). The socioecology of primate groups. *Annual Review of Ecology and Systematics, 17*, 111-135.

Terborgh, J., & Janson, C.H. (1983). Ecology of primates in southeastern Peru. *National Geographic Society Research Reports, 15*, 655-662.

Thompson, W.A., Vertinsky, I., & Krebs, J.R. (1974). The survival value of flocking in birds: A simulation model. *Journal of Animal Ecology, 43*, 785-820.

Thorington, R.W., Jr. (1976). The systematics of New World monkeys. In First Inter-American Conference on Conservation and Utilization of American Nonhuman Primates in Biomedical Research, Pan American Health Organization Sci. Publ., 317 (pp. 8-18). Washington, D.C.: Pan American Health Organization (PAHO), World Health Organization (WHO).

Thorington, R.W., Jr. (1988). Taxanomic status of *Saguinus tripartitus* (Milne-Edwards, 1878). *American Journal of Primatology, 15*, 367-371.

Thorndike, E.L. (1898). Animal intelligence: An experimental study of the associative process in animals. *Psychological Review Monograph, 2 (Suppl. 4)*, 1-109.

Thorpe, W.H. (1963). *Learning and Instinct in Animals*. London: Methuen.

Tinbergen, N. (1958). *Curious Naturalists*. New York: Basic Books.

Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signalling of chimpanzees? In S.T Parker & K.R.G. Gibson (Eds.), *"Language" and Intelligence in Monkeys and Apes: Comparative developmental perspectives* (pp. 274-311). Cambridge: Cambridge University Press.

Tomasello, M. (1996). Do apes ape? In C.M. Heyes & B.G. Galef (Eds.), *Social Learning in Animals* (pp. 319-346). San Diego: Academic Press.

Tomasello, M., & Call, J. (1997). *Primate Cognition.* Oxford: Oxford University Press.

Tolman, E.C. (1948). Cognitive maps in rats and men. *Psychological Review, 55,* 189-208.

Tolman, E.C. (1959). Principles of Purposive Behaviour: In S. Koch (Ed.), *Psychology: A study of a science, Vol. 2., General systematic formulations, learning and special processes* (pp. 92-157). London: McGraw-Hill Book Company Inc.

Treisman, M. (1975a). Predation and the evolution of gregariousness I: Models for concealment and evasion. *Animal Behaviour, 23,* 779-800.

Treisman, M. (1975b). Predation and the evolution of gregariousness I: An economic model for predator-prey interaction. *Animal Behaviour, 23,* 801-825.

Trivers, R.L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology, 46,* 35-37.

Turner, E.R.A. (1964). Social feeding in birds. *Behaviour, 24,* 1-46.

Ungar, P.S. (1996). Feeding height and niche separation in sympatric monkeys and apes. *Folia Primatologica, 67,* 163-168.

Valone, T.J. (1989). Group foraging, public information and patch estimation. *Oikos, 56,* 357-363.

Valone, T.J. (1991). Bayesian and prescient assessment foraging with pre-harvest information. *Animal Behaviour, 41,* 569-577.

Valone, T.J. (1992). Information for patch assessment: a field investigation with black-chinned hummingbirds. *Behavioural Ecology, 3,* 211-222.

Valone, T.J., & Brown, J.S. (1989). Measuring patch assessment abilities of desert granivores. *Ecology, 70,* 1800-1810.

Valone, T.J., & Giraldeau, L.-A. (1993). Patch estimation by group foragers: what information is used? *Animal Behaviour, 45*, 721-728.

Van Schaik, C.P. (1983). Why are dirunal primates living in groups? *Behaviour, 87*, 120-156.

Van Schaik, C.P., & van Hoof, J.A.R.A.M. (1983). On the ultimate causes of primate social systems. *Behaviour, 85*, 91-117.

Van Schaik, C.P., van Noordwijk, M.A., de Boer, R.J., & den Tonkelaar, I. (1983). The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fasicualris*). *Behavioural Ecology and Sociobiology, 13*, 173-181.

Vine, I. (1971). Risk of visual detection and pursuit by a predator and the selective advanatge of flocking behvaiour. *Journal of Theoretical Biology, 30*, 405-422.

Visalberghi, E. (1994). Learning processes and feeding behaviour in monkeys. In B.G. Galef, M. Mainardi, & P. Valsecchi (Eds.), *Behavioural Aspects of Feeding: Basic and applied research on mammals* (pp. 257-270). Chur, Switzerland: Harwood Academic Publishers.

Visalberghi, E. & Fragaszy, D. (1995). The behaviour of capuchin monkeys (*Cebus apella*) with food: The role of social context. *Animal Behaviour, 49*, 1089-1095.

Visalberghi, E., & Fragaszy, D.M. (1996). Pedagogy and imitation in monkeys: Yes, no or maybe? In D.R. Olson & N. Torrance (Eds.), *The Handbook of Education and Human Development* (pp. 277-301). Cambridge, Massachusetts: Blackwell.

Visalberghi, E., Valente, M., Fragaszy, D. (1998). Social context and consumption of unfamiliar foods by capuchin monkeys (*Cebus apella*) over repeated encounters. *American Journal of Primatology, 45*, 367-380.

Vitale, A., & Queyras, A. (1997). The response to novel foods in common marmoset (*Callithrix jacchus*): the effects of different social contexts. *Ethology, 103*, 395-403.

Vivo, M., de (1985). On some monkeys from Rondônia, Brasil (Primates: Callitrichidae, Cebidae). *Papeis Avulsos Zool., São Paulo, 36*, 103-110.

Vogt, J.L. (1978). The social behavior of a marmoset (*Saguinus fuscicollis*) group II: behavior patterns and social interaction. *Primates, 19*, 87-300.

Wachter, B., Schabel, M., & Noë, R. (1997). Diet overlap and ployspecific associations of red colobus and Diana monkeys in Tai National Park, Ivory Coast. *Ethology, 103*, 514-526.

Ward, P., & Zahavi, A. (1973). The importance of certain assemblages of birds as "information centers" for food finding. *Ibis, 115*, 517-534.

Waser, P.M. (1977). Feeding, ranging, and group size in the mangabey Cercocebus a albigena. In T.H. Clutton-Brock (Ed.), *Primate Ecology*. London: Academic Press.

Waser, P.M. (1982). Primate polyspecific associations: do they occur by chance? *Animal Behaviour, 30*, 1-8.

Waser, P.M. (1987). Interactions among primate species. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate Societies* (pp. 210-226). Chicago: University of Chicago Press.

Waser, P.M., & Case, T.J. (1981). Monkeys and matrices: on the coexistence of "omnivorous" forest primates. *Oecologia, 49*, 102-108.

Washburn, D.A., & Rumbaugh, D.M. (1991). Rhesus monkey (*Macaca mulatta*) complex learning-skills reassessed. *International Journal of Primatology, 12*, 377-388.

Watts, D.P. (1985). Observations on the ontogeny of feeding behavior in mountain gorillas (*Gorilla gorilla beringei*). *American Journal of Primatology, 8*, 1-10.

Weigl, P.D., & Hanson, E.V. (1980). Observational learning and the feeding behavior of the red squirrel *Tamiasciurus hudsonicus*: the ontogeny of optimisation. *Ecology, 61*, 213-218.

West Eberhard, M.J. (1975). The evolution of social behavior by kin selection. *Quarterly Review of Biology, 50*, 1-33.

Whitehead, J.M. (1986). Development of feeding selectivity in mantled howling monkeys, *Alouatta palliata*. In J.G. Else & P.C. Lee (Eds.), *Primate Ontogeny, Cognition and Social Behavior*. (pp. 105-117). Cambridge: Cambridge University Press.

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. In P.J.B. Slater, J.S. Rosenblatt, C. Beer & M. Milinski (Eds.), *Advances in the Study of Behavior, Vol. 21* (pp. 239-283). New York: Academic Press.

Whitesides, G.H. (1981). *Community and population ecology of non-human primates in the Douala-Edea Forest Reserve.* Unpublished M.Sc. thesis, The Johns Hopkins University, Baltimore, Maryland.

Whitesides, G.H. (1989). Interspecific associations of Diana monkeys, *Cercopithecus diana*, in Sierra Leone, West Africa: Biological significance or chance? *Animal Behaviour, 37*, 760-776.

Widowski, T.M., Ziegler, T.E., Elowson, M.A., & Snowdon, C.T. (1990). The role of males in the stimulation of reproductive function in female cotton-top tamarins *Saguinus oedipus*. *Animal Behaviour, 40*, 731-741.

Wilkinson, G.S. (1992). Information transfer at evening bat colonies. *Animal Behaviour, 44*, 501-508.

Windfelder, T.L. (1997). *Polyspecific association and inter-specific communication between two Neotropical primates: Saddle-back tamarins* (Saguinus fuscicollis) *and emperor tamarins* (Saguinus imperator). Unpublished Ph.D. thesis, Duke University, Durham.

Wolf, N.G. (1985). Odd fish abandon mixed-species groups when threatened. *Behavioural Ecology and Sociobiology, 17*, 47-52.

Wolfe, L.G., Deinhardt, F., Ogden, J.D., Adams, M.R., & Fischer, L.E. (1975). Reproduction of wild-caught and laboratory-born marmoset species used in biomedical research (*Saguinus* sp., *Callithrix jacchus*). *Laboratory Animal Care, 25*, 802-813.

Wrangham, R.W. (1980). An ecological model of female primate groups. *Behaviour, 75*, 262-300.

Wrangham, R.W. (1983). Social relationships in comparative perspective. In R.A Hinde (Ed.), *Primate Social Relationships: An integrated approach* (pp. 255-262). Oxford: Blackwell.

Wrangham, R.W. (1987). Evolution of social structure. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.). *Primate Societies* (pp. 282-296). Chicago: University of Chicago Press.

Wrangham, R.W., Gittlema, J.L., & Chapman, C.A. (1993). Constraints on group size in primates and carnivores: population density and day range as assays of exploitation competition. *Behavioural Ecology and Sociobiology, 32*, 199-209.

Yamamoto, M.E. (1993). From dependence to sexual maturity: the behavioural ontogeny of Callitrichidae. In A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology* (pp. 235-254). Oxford: Oxford University Press.

Yoerg, S.I. (1991). Social feeding reverses learned flavour aversions in spotted hyenas (*Crocuta crocuta*). *Journal of Comparative Psychology, 105*, 185-189.

Yoneda, M. (1981). *Ecological studies of* Saguinus fuscicollis *and* S. labiatus *with reference to habitat segregation and height preference.* Kyoto University Overseas Research Report of New World Monkeys, II, 43-50.

Yoneda, M. (1984a). Comparative studies on vertical separation, foraging behavior and travelling mode of saddle-backed tamarins (*Saguinus fuscicollis*) and red-chested moustached tamarins (*Saguinus labiatus*) in Northern Bolivia. *Primates, 25,* 414-422.

Yoneda, M. (1984b). Ecological study of the saddle backed tamarin (*Saguinus fuscicollis*) in northern Bolivia. *Primates, 25*, 1-12.

Zach, R., & Falls, J.B. (1976). Do Ovenbirds (Aves: Parulidae) hunt by expectation? *Canadian Journal of Zoology, 54*, 1894-1903.

Zahavi, A. (1971). The function of pre-roost gatherings and communal roosts. *Ibis, 113*, 106-109.

Zajonc, R.B. (1965). Social facilitation. *Science, 149*, 269-274.

Zentall, T.R., & Galef, B.G. (1988). *Social Learning: Psychological and Biological Perspectives.* Hillsdale, New Jersey: Lawrence Erlbaum.

Ziegler, T.E., Epple, G., Snowdon, C.T., Porter, T.A, Belcher, A.M., & Kudërling, I. (1993). Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus*. *Animal Behaviour, 45*, 313-322.

Zullo, J., & Caine, N.G. (1988). The use of sentinels in captive groups of red-bellied tamarins. *American Journal of Primatology, 14*, 455. (Abstract).

Appendix: List of Species

Accipiter bicolor (bicoloured hawk)
Alouatta palliata (mantled howler monkey)
Alouatta sara (Bolivian red howler monkey)
Alouatta seniculus (red howler monkey)
Aotus nigriceps (night monkey)
Ateles geoffroyi (black-handed spider monkey)
Bertholletia excelsa (Brazil nut)
Bycanistes subcylindricus (black-and-white casqued hornbill)
Callicebus brunneus (brown titi monkey)
Callimico goeldii (Goeldi's monkey)
Callithrix argentata (silvery/bare-ear marmoset)
Callithrix emiliae (Snethalge's marmoset)
Callithrix geoffroyi (Geoffroy's tufted-ear marmoset)
Callithrix jacchus (common/white tufted-ear marmoset)
Callithrix kuhli (Wied's black-tufted-ear marmoset)
C. penicillata (black-tufted ear marmoset)
Cassia grandis (horse cassia)
Cebuella pygmaea (pygmy marmoset)
Cebus albifrons (white-fronted capuchin)
Cebus apella (tufted capuchin)
Cebus capucinus (white-faced capuchin)
Cercopithecus aethiops (vervet monkey)
Cercopithecus ascanius (red-tailed monkey)
Cercopithecus diana (Diana monkey)
Ceropithecus mitis (blue monkey)
Colobus badius (red colobus)
Crocuta crocuta (spotted hyena)
Daptrius americanus (red-throated caracara)
Eira barbara (tayra)
Esox lucius (pike)

Felis pardalis (ocelot)
Gorilla gorilla beringei (mountain gorilla).
Junco hyemalis (dark-eyed junco)
Leontopithecus chrysomelas (golden-headed lion tamarin)
Leontopithecus rosalia (golden lion tamarin)
Loligo vulgaris (squid)
Lophocebus albigena (gray-cheeked mangabey)
Macaca fuscata (Japanese macaque)
Macaca mulatta (rhesus macaque)
Macaca nemestrina (pig-tailed macaque)
Mandrillus sphinx (mandrill)
Micrastur ruficollis (barred forest-falcon)
Pan troglodytes (common chimpanzee)
Papio cynocephalus (yellow baboon)
Papio papio (Guinea baboon)
Papio ursinus (Chacma baboon)
Parus atricapillus (black-capped chickadee)
Parus major (great tit)
Parus rufescens (chestnut-backed chickadee)
Passer domesticus (house sparrow)
Perca fluviatilis (perch)
Pitheca irrorata (Gray's bald-faced saki)
Procolobus versus (olive colobus)
Rattus norvegicus (Norway rat)
Saguinus bicolor (pied/bare-faced tamarin)
Saguinus fuscicollis (saddle-backed tamarin)
Saguinus geoffroyi (Geoffroy's tamarin)
Saguinus imperator (emperor tamarin)
Saguinus labiatus (red-bellied tamarin)
Saguinus midas (golden-handed tamarin)
Saguinus mystax (moustached tamarin)
Saguinus nigricollis (black-mantled tamarin)

Saguinus oedipus (cotton-top tamarin)

Saguinus triparitus (golden-mantled saddle-backed tamarin)

Saimiri boliviensis (Bolivian squirrel monkey)

Saimiri oerstedii (red-backed squirrel monkey)

Saimiri sciureus (common squirrel monkey)

Sepia officinalis (cuttlefish)

Spizaetus ornatus (ornate hawk-eagle)

Stephanoaetus coronatus (crowned eagle)

Symphonia globulifera (ossol)

Tamiasciurus hudsonicus (red-squirrel)

Tenebrio mollitor (flour beetle)