Living Together: Habitat use, behaviour, and social networks in mixed-species groups of tufted capuchin and squirrel monkeys

Sophia Marieangela Daoudi-Simison

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DECLARATION

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text. It has not been previously submitted, in part or whole, to any university or institution for any degree, diploma, or other qualification.

In accordance with the University of Stirlng 'code of practice: research degrees', this thesis does not exceed 80,000 words.

Signed: S.Daoudi-Simison
Sophia Marieangela Daoudi-Simison

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ABSTRACT

Mixed-species groups, which represent a special mode of “group-living” have been described in a number of taxa, however there is no consensus as to how these groups are defined and measured: (1) some authors refer to a collective noun (e.g. ‘group’, ‘flock’, ‘troop’, ‘aggregation’) without explicitly defining the term; (2) some authors provide general definitions based on behaviour and interactions that are not explicitly measured and 3) some provide quantifiable definitions based on distances, but the distances appear arbitrary. There are four prerequisites that constitute “groupness”: (1) group stability; (2) an element of socialness; (3) proximity and behavioural coordination in time and space and; (4) a minimum number ≥2. I review the literature on single-species and mixed-species animal groups, focussing on the costs and benefits of groups in relation to the two main selective forces that drive grouping and ultimately lead to improved fitness in animals: foraging advantages and reduced risk of predation. This thesis uses a multi-methodological approach of field and captive observations, in order to quantify the ‘groupness’, of mixed-species groups of Guianan brown capuchins (*Sapajus apella*) and Guianan squirrel monkeys (*Saimiri sciureus*), based on the four aforementioned prerequisites for grouping. My fieldwork in Suriname, South America, at two study sites showed extensive variability but overall, the species were rarely in proximity. I collected behavioural data on two mixed-species groups of *Sapajus* and *Saimiri* at the Living Links to Human Evolution Research Centre, RZSS, Edinburgh Zoo. I investigated the groupness of the monkeys in both single-species and mixed-species groups, using different methodological approaches to quantify the different prerequisites of grouping. Prerequisite (3) was examined via 3D space use in enclosures (proximity in time and space) and group behavioural synchrony (coordination in time and space). Prerequisites (1) and (2) were examined using social network analysis. *Sapajus* and *Saimiri* occupied different spaces in their shared enclosures, their behaviours were largely asynchronous and social networks produced two distinct species clusters. I conclude that *Sapajus* and *Saimiri* were not behaving as true mixed-species groups, and that there is fluidity in patterns. In addition to the theoretical interest in understanding mixed-species groups, this thesis explores how the findings relate more generally to welfare in captivity and provides operational definitions that distinguish mixed-species groups from mixed-species associations and aggregations.

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1 GENERAL INTRODUCTION

Prior to considering mixed-species animal groups it is first essential to consider what a single-species group is and what factors/parameters are necessary for animals to be considered a group. The following chapter is in two parts; firstly I discuss the existing literature on single- and mixed-species animal groups; and secondly I provide details on the study genera (capuchins: *Cebus/Sapajus* spp. and squirrel monkeys: *Saimiri* spp.) and study species (Guianan brown capuchin: *Sapajus apella* and Guianan squirrel monkey *Saimiri sciureus*).

PART I: Animal groups

1.1 What is an animal group?

Understanding why animals live in groups is an important and complex issue within the study of animal behaviour. It is commonly accepted within the natural sciences that a population is defined as all members of a single species that exist in a given habitat at the same time and are able to interbreed (Dempster, 1975; Barbour, Burk & Pitts, 1987; Ricklefs & Relyea, 2014; Viscido & Shrestha, 2015). However, there is currently no equivalent consensus for defining an animal group. When considering animal groups, we may be inclined to think of the visually dramatic phenomena of coordinated movements in large herds, flocks, swarms or shoals, or aggregations around a resource (e.g. a watering hole). Conversely, we may think of groups in terms of their different collective names such as a school of fish, a pod of whales, a colony of ants, or a troop of monkeys. Many definitions provided are vague and difficult to apply across species. For instance, Lee (1994, p. 266) notes that while a simple definition of a group such as *"When two or more animals live together they constitute a social unit"* is relatively straightforward, it ignores the different and complex ways in which animal groups/societies live (e.g. fission-fusion societies). Moreover, when further examining the existing literature on animal groups there appear to be three broad categories of studies: (1) those that provide a general definition of 'group' that is unquantifiable in any precise way; (2) those that refer to a 'group' (or flock, herd, troop etc) without providing a definition and; (3) those that are quantifiable but often not quantified in relation to criteria. Examples of the latter category are Wilson (1975, p. 8) who defined a group as "*a set of organisms belonging to the same species that remain together for any period of time while interacting with one another to a much greater degree than with other conspecific organisms"*; Parrish and Hammer (1997, p. 1) *"…when our congregations of creatures are behaviorally coordinated in space and time, synchronously moving and wheeling and twisting before us in three-dimensional space..."* and; Ward and Webster (2016, p. 2) *"where two or more individuals maintain proximity in space and time through the mechanism of social attraction"*.

For all the above definitions, there seems to be a general agreement on the essential prerequisites for 'grouping' – namely that there is: (1) group stability, (2) an element of socialness (Thorndike & Stein, 1937; Tokunaga & Mitchell, 1977) that is, interactions (3) proximity and behavioural coordination in time and space, and (4) a minimum of two individuals. The first three require elaboration on how to define and measure whether these prerequisites are met. The first, 'group stability', relates to when the configuration of the group remains recognisable irrespective of individuals joining or leaving the group (i.e. the position of the individual may change relative to each other, but there is some continuity of some individuals over time). The second, 'an element of socialness', may be directly observed by social attraction (i.e. individuals seek out the presence of others in the group, which also serves to maintain the group), and social interaction; which can be direct physical interaction (and physical proximity can also be used as a proxy measure here), or through other means such as vocal communication. Given the need for social attraction, some of these interactions are likely to be positive (e.g. play or grooming). This leads to the third essential factor, proximity and behavioural coordination in time and space, whereby individuals are essentially doing the same things at the same time and within a 'meaningful' distance that enables both direct and indirect communication (i.e. verbal or visual) and/or interactions. It is also important to distinguish between groups, associations, and temporary aggregations around a resource (see also Section 1.4).

By elaborating on these prerequisites for grouping they allow for the complexity of the different social tendencies and modes in which some animals live, such as fission-fusion communities and exclude temporary aggregations around a resource. Previous authors have criticised definitions of group-living for not allowing for these complex social tendencies (Partridge, 1981, 1982; Lee, 1994; van Schaik, 1999; Ward & Webster, 2016). For instance, Pitcher, Magurran and Allan (1983) note that in order for groups to be able to communicate and coordinate their behaviours, they will need to be within 4-5 body lengths to enable continuous information exchange with other group members. While this does meet two of the prerequisites for grouping, they have provided a specific proximal distance that would be difficult to apply to multiple species, for example humpback whales (*Megaptera novaeangliae*) can communicate acoustically over distances as far as 160km (i.e. much further than 4-5 body lengths - Tyack, 1982; Winn & Winn, 1985; Clark, 1995; Mercado III & Frazer, 1999; Mercado III, 2016). Animals that are described as being solitary (i.e. mostly leading independent lives), will need to come together (socially interact) in order to mate, and for females there may be periods of parental care (e.g. sloths (*Bradypus* spp., *Choloepus* spp.), lorises (*Nycticebus* spp., *Loris* spp.) and snow leopards (*Panthera uncia*) – see review in Lee, 1994). Therefore, based on the above prerequisites, solitary animals that are mating or carrying offspring could be considered to be a group (at least temporarily). Furthermore, animals housed together in captivity (e.g. zoo or laboratory) are often considered to be living in groups, as they would usually be in proximity in three-dimensional time and space, and interact with each other, however it may be difficult to determine whether this 'group membership' is due to 'social attraction' or merely due to living in a confined space (e.g. Stankowich, 2003; Viscido & Shrestha, 2015).

While I do not apply any of the aforementioned definitions to my studies in this thesis, it is still important to consider the criteria that are given as essential prerequisites for grouping. However, it is difficult to find any objective or quantifiable means to determine whether individuals in a set of animals (wild or captive) observed in various locations, range of proximities, and forms of conspecific interactions are all members of a single group. But perhaps searching for an all-encompassing definition that includes all of the prerequisites, is not the answer, in fact most attempts tend to result in a sterile list of criteria that remain difficult to apply across species (Krause & Ruxton, 2002; Lee, 1994; Viscido & Shrestha, 2015). Therefore, given the diversity of animal grouping behaviour, it would be more prudent to develop more operational definitions that fit with both the study species and the research question(s) being investigated. In this thesis I provide examples of different methodological approaches where "groupness" (Lorge, 1955; Campbell, 1958) can be tested and quantified in accordance with one or more of the above prerequisites (see Section 1.4). However, before we delve more into this, it is first important to understand why animals form groups.

1.2 Why live in a group?

In order to gain a better understanding of how group-living evolved, it is necessary to determine the impact of the environment, in addition to the types of interactions and associations between individuals, and to discuss the resulting modes of sociality in relation to the costs and benefits of grouping (Altmann, 1974a; Wilson, 1975; Bertram, 1978; van Schaik, 1983; Wrangham & Rubenstein, 1986; Dunbar, 1988; Lee, 1994; Smith & Szathmáry, 1995; Krause & Ruxton, 2002; Davies, Krebs & West, 2012; Ward & Webster, 2016). The selection pressures that may have favoured grouping include: (1) foraging advantages via increased energy uptake via increased efficiency in foraging, defence of resources and social learning (e.g. collective memory for scarce resources such as waterholes); (2) reduced risk of predation (e.g. more ears and eyes, dilution effect, selfish herd effect, improved rate of detection); (3) improved opportunities for mating; (4) increased survival of offspring via synchronised births and alloparenting; (5) reduction of parasite load due to grooming (see also Table 1.1). However, it should be noted that each of the benefits mentioned may also have some associated costs (Wilson, 1975; Bertram, 1978; van Schaik, 1983; Wrangham & Rubenstein, 1986; Dunbar, 1988; Lee, 1994; Smith & Szathmary, 1995; Krause & Ruxton, 2002; Davies et al., 2012, see also Table 1.1). Clearly there are situations in which group-living would be more advantageous than living alone and depending on the balance between the costs and benefits of grouping, there may likewise be instances where being a lone individual is more beneficial. But the advantages must outweigh the costs as group-living is common amongst animals in general, and amongst the primates ~90% of species are considered to live in groups (e.g. Isbell, 1994; Fleagle, 1999; Strier, 2007; Parga

& Overdorff, 2011), though if we include mother-infant and mating pairs as forming temporary groups then we could say 100%.

When discussing the costs and benefits of group-living it is important to also consider the variation (between and within species) in group formation (e.g. seasonal and environmental effects), group size (e.g. when and where groups of different sizes are established), group composition (e.g. how individuals affect group cohesion, how individuals in the group interact, which individuals aggregate), and the stability and maintenance of the group over time (Caraco, 1979, 1981; van Schaik & van Hoof, 1983; Lee, 1994; Janson & Goldsmith, 1995; Parnell, 2002; Grove, 2012). There is an inextricable link between the factors that affect group formation and group size, and often this cannot be solely explained by a simple description of the cost/benefit ratios (Lee, 1994). That being said, when investigating group-living the primary interest tends to focus on the costs and benefits which allow for the maintenance of grouping (Dunbar, 1988; Lee, 1994; Zemel & Lubin, 1995; Krause & Ruxton, 2002). The benefits derived from grouping (e.g. cooperation, enhanced foraging efficiency, reduced predation risks) increase at a diminishing rate, and so once a group gets above a certain size the benefit per individual decreases as more members join due to increased competition for resources. In earlier investigations (e.g. Caraco & Wolf, 1975; Wilson, 1975; Rodman, 1981), animals were expected to forage in groups of ‘optimal’ size (i.e. that corresponded to their maximum average fitness). However, field observations showed that groups tended to be larger than the predicted optimal sizes (Rodman, 1981; Pulliam & Caraco, 1984). Indeed it became clear that individuals would continue to join an ‘overpopulated’ group (with members tending not to leave) so long as the individual fitness of group members exceeded that of a solitary forager (Sibly, 1983; Clark & Mangel, 1984).

I will be focussing on the two main selective forces for animal groups (that are susceptible to predation) noted extensively in the existing literature: (1) foraging advantages, and; (2) reduced risk of predation (Wilson, 1975; Bertram, 1978; van Schaik, 1983; Wrangham & Rubenstein, 1986; Dunbar, 1988; Lee, 1994; Smith & Szathmary, 1995; Krause & Ruxton, 2002; Davies et al., 2012; Ward & Webster, 2016).

Table 1.1 *Summary of potential benefits and costs of group-living compared to solitary living (adapted from Lee, 1994; Ward & Webster, 2016).*

Functional category	**Benefits of grouping**	**Costs**
*Foraging (and other resources)	Defence of food patches (and other key resources such as sleeping sites, waterholes etc), efficiency in food location, shared information about quality, co-operative hunting, scrounging from other group members	Competition for shared resources (reduced intake per individual), increased energy costs (e.g. may need to travel further to find food patches or prey), other group members stealing food, spying/parasitism and kleptoparasitism
*Predation	Dilution effects, selfish herd, confusion effects, mobbing, reduced time spent vigilant (per individual – more ears and eyes), increased chance of detecting a predator	More conspicuous (audibly and visually) increasing chances of predator detection
Access to mates	Opportunities to gain access to mates and reduced search costs	Direct or indirect competition for access to mates, potential for infanticide (to increase access to reproductive females)
Alloparenting (helpers for rearing infants)	Additional protection of vulnerable infants, reduced maternal energy costs, synchronisation of breeding, social learning for juveniles	Potential for infanticide, kidnapping, cannibalism, delayed dispersal and reproduction by helpers
Pathogens & parasites	Opportunities to reduce parasite loads through grooming	Increased transmission, probability of morbidity, susceptible to higher parasite loads

*focal themes of this thesis

What determines the nature, size and temporal stability of a "group" will thus be expected to be a complex interaction between local costs and benefits for each context; how influential is each benefit for survival and reproduction, and how detrimental is each cost. Despite the complexity of balancing costs and benefits, the key driver of reproduction is food supply for females, while the key driver of survival is not being eaten. Thus, throughout this thesis, I will focus on foraging and predation as potentially the most significant selective forces driving group-living.

1.3 Why form mixed-species groups?

Mixed-species groups are composed of two or more species, and are referred to in the literature in a number of ways: multispecies groups (Wing, 1946), mixed-species groups (Eaton, 1953), interspecific groups (Rice, 1956), polyspecific associations (Gartlan & Struhsaker, 1972), heterospecific groups (Morse, 1977), and mixed-species associations (Powell, 1985 see also reviews in Stensland, Anderbjörn & Berggren, 2003; Goodale, Beauchamp & Ruxton, 2017). For the purpose of this thesis, and for consistency I will (where possible) use the term mixed-species groups. For the most part, mixed-species groups tend to include species from related taxa (e.g. ungulates on the savannah: Fitzgibbon, 1990, 1994; Pays, Ekori & Fritz, 2014; primates in various forest types: Struhsaker, 1981; Terborgh, 1983; Cords, 1987; Whitesides, 1989; Peres, 1992, 1993a; Chapman & Chapman, 2000b; and cetaceans in various marine habitats: Shelden, Baldridge & Withrow, 1995; Herzing & Johnson, 1997; Zaeschmar, Dwyer & Stockin, 2013). However, there have been instances where non-related taxa have been observed forming mixed-species groups (e.g. Indian Hanuman langurs (*Presbitis entellus*) and chital deer (*Axis axis*): Newton, 1989; double-toothed kites (*Harpagus bidentatus*) and white-headed capuchins (*Cebus capucinus*), and grey-headed tanagers (*Eucometis pencillata*) and the Central American squirrel monkey (*Saimiri oerstedii*): Boinski & Scott, 1988). Mixed-species groups can vary in their duration, frequency, activities, and structure, depending on the species combinations, and as such it can be difficult to determine their stability and function (Cords, 1987; Stensland et al., 2003). Especially as established in the previous section, it can be costly to live in groups (see Table 1.1) and so it seems counterintuitive to increase group size by including another species, which could result in increased competition for potential resources (e.g. food, water, sleeping sites). That being said, selection must favour the formation of mixed-species groups so long as the individual fitness of its members exceeds that of a single-species group (Gautier-Hion, Quris & Gautier, 1983). Thus the main hypotheses proposed for mixed-species groups are essentially the same as for single-species (see previous sections), and although they are unlikely to involve all of the same advantages such as offspring-viable mating opportunities and genetic relatedness (Hamilton, 1964; Altmann, 1974a; Wilson, 1975; Bertram, 1978; Wrangham & Rubenstein, 1986; Dunbar, 1988; Lee, 1994; Smith & Szathmáry, 1995; Krause & Ruxton, 2002; Davies et al., 2012; Ward & Webster, 2016), the formation of mixed-species groups may provide individuals with evolutionary benefits that would be unattainable in single-species groups (Whitesides, 1989; Heymann & Buchanan-Smith, 2000; Stensland et al., 2003).

1.3.1 Increased foraging efficiency vs feeding competition

There are a number of benefits that can be derived from foraging in a group (Table 1.1), for instance an individual can, for the most part, utilise resources more efficiently as a member of a group than it could as a lone individual (e.g. Altmann, 1974a, 1974b; Wrangham, 1980; 1987; Caraco, 1981; van Schaik, 1983; Lee, 1994; Krause & Ruxton, 2002; Ward & Webster, 2016). Group-living animals can spend more time foraging by sharing the costs of being vigilant against predators, and can cooperate in defending food patches from other individuals, or groups (van Schaik, 1983; de Ruiter, 1986; Rose & Fedigan, 1995; Eckardt & Zuberbühler, 2004; Davies et al., 2012; Brown, 2013). Decisions governing foraging in groups may also be more efficient via social learning, such as transmission of information in relation to the location of food sites (e.g. honey bees (*Apis mellifera*), von Frisch, 1967; Beekman & Ratnieks, 2001), and the abundance and/or quality of foods available (e.g. spider monkeys (*Ateles geoffroyi*), Chapman & Lefebvre, 1990; bonobos (*Pan paniscus*), Clay & Zuberbühler, 2009). Furthermore, grouping may also reduce the variance in times between obtaining food, thus maximising renewal time (i.e. systematically using resources) and avoiding areas that have been previously utilised/foraged (e.g. Cody, 1971; Altmann, 1974a; Clutton-Brock, 1974; Ruxton, Hall & Gurney, 1995; Giraldeau & Beauchamp, 1999; Krause & Ruxton, 2002). This in turn will save the energetic expenses of travelling to unprofitable feeding locations and in turn may reduce the risk of predation incurred by extra travel.

The formation of mixed-species groups may facilitate the task of searching for food (e.g. von Frisch, 1967; Chapman & Lefebvre, 1990; Beekman & Ratnieks, 2001; Clay & Zuberbühler, 2009), so long as there is dietary similarity between the different species (e.g. Fleagle & Mittermeier, 1980; Terborgh, 1983; Norconk, 1986). Therefore, if individuals from one group are able to capitalise on the knowledge and skills of another presumably more experienced group (i.e. through either sharing or parasitism of information – social learning) then this will likely increase foraging efficiency (Gartlan & Struhsaker, 1972; Struhsaker, 1981; Gautier-Hion et al., 1983; Terborgh, 1983; Cords, 1987; Lee, 1994). Furthermore, forming associations with another species may enable access to formerly unknown foraging sites, especially if home ranges are substantially different in size. For instance, the species occupying the larger home range may benefit from the superior knowledge of the species occupying the smaller home range by using them as guides to resources (Gartlan & Struhsaker, 1972; Terborgh, 1983; Cords, 1990a; Podolsky, 1990). For example, Terborgh (1983) noted that in mixed-species groups of black-capped squirrel monkeys (*Saimiri boliviensis* - formerly known as common squirrel monkey, *Saimiri sciureus* – see updated review on taxonomy in Rylands & Mittermeier, 2013) and large-headed capuchins (*Sapajus macrocephalus* - formerly brown tufted capuchin *Cebus apella* – see Rylands & Mittermeier, 2013), the former (who had larger home ranges) were following ~three different *Sapajus* groups (with smaller home ranges), and in times of food scarcity *Sapajus* groups would follow *Saimiri*. Furthermore, by forming mixed-species groups, species may gain access to potentially otherwise unavailable food. For example, *Saimiri* were observed scavenging partially eaten *Scheela* nuts (ordinarily inaccessible to them) dropped by *Sapajus* (Terborgh, 1983; Podolsky, 1990). Similarly, mixed-species groups may increase their prey capture rates as a result of the beating effect, whereby one species is able to gain food items (usually insects) flushed out by the movement of the other species (Gartlan & Struhsaker, 1972; Klein & Klein, 1973; Pook & Pook, 1982; Terborgh, 1990).

The above mechanisms enable individuals to reap the benefits of grouping, compared to what they may be able to achieve from being solitary. However, individuals may also incur some associated costs by grouping (e.g. Wrangham, 1979, 1980; van Schaik, 1983; Dunbar 1988; Lee, 1994; Krause & Ruxton, 2002; Ward & Webster, 2016 – also see Table 1.1). For example, larger groups can result in increased competition for resources, to the extent that the costs of grouping outweigh the benefits. The ecological constraints hypothesis (Emlen, 1984, 1994) proposes that larger group sizes will increase within-group feeding competition, necessitating individuals to visit more food patches (so as to satisfy the energy requirements of group members), and cover greater distances than they would in smaller groups or as solitary individuals (Altmann, 1974b; Chapman, 1990; Wrangham, Gittleman & Chapman, 1993; Chapman & Chapman, 2000a; Grove, 2012).

Furthermore, Alexander (1974) states that increased feeding competition is an automatic and universal consequence of grouping. For instance, synchronization of feeding activities will likely result in an increase in interference competition (i.e. direct aggressive interactions between competitors for food items), and exploitative competition (i.e. competitors denying each other access to a resource by depleting – indirect interaction) when there is joint use of resources in a given area (e.g. Isbell, 1991; Janson, 1988; Snaith & Chapman, 2005; Vogel, 2005; Itoh & Nishida, 2007). In contrast, Rubenstein (1978) argues that competition is not necessarily automatic and is only an issue if resources are limited, and with regard to mixed-species groups, if the species share the same diet. Therefore, in order for mixed-species grouping to be beneficial there would need to be less feeding competition than would be expected in a similar sized single-species group (e.g. Caldwell, 1981; Peres, 1993b; Stensland et al., 2003; Goodale et al., 2017). For the most part studies on primate mixed-species groups note that competition is not exacerbated in them, either due to no interspecific aggression having been observed (e.g. Bernstein, 1967; Gautier & Gautier-Hion, 1969; Gautier-Hion & Gautier, 1974); or because food was abundant (e.g. Gartlan & Struhsaker, 1972); or due to ecological niche partitioning (e.g. Fleagle & Mittermeier, 1980; Terborgh, 1983; Podolsky, 1990; Buchanan-Smith, 1999a).

1.3.2 Decreased risk of predation

As with single-species groups, forming larger mixed-species groups enables members to better detect predators due to there being more ears and eyes present (e.g. Pulliam, 1973; van Schaik, 1983; Stensland et al., 2003). However, the efficacy of this mechanism will depend on the ability of the two species to understand and take heed of the warning signals (e.g. alarm vocalisations, escape behaviours) of the other (Pulliam, 1973; Elgar, 1989; Lima, 1990, 1995; Lehtonen & Jaatinen, 2016). For example, there are different types of calls/vocalisations for different predators (e.g. terrestrial and aerial), and if one species vocalizes due to an aerial predator and the other species look to the ground then the warning signal would benefit only one species (e.g. Rowell & Hinde, 1962; Byrne, 1982). However, interspecific responses to warning signals have been documented across primate taxa (e.g. Struhsaker, 1970; Terborgh, 1983; Buchanan-Smith, 1990; Heymann, 1990b; Seyfarth & Cheney, 1990; Oda & Masataka, 1996; Sussman, 2000, 2003; Zuberbühler, 2000a, 2000b; Fitchel, 2004). Playback experiments on a group of captive ring-tailed lemurs (*Lemur catta*) found that despite having never previously heard Verreaux's sifakas (*Propithecus verreauxi*) raptor alarm calls, they responded appropriately by looking up into the sky (Oda & Masataka, 1996). A further benefit of the increased number of attentive eyes and ears in larger single- and mixed-species groups, allows individuals to spend less time engaging in vigilant behaviours compared to a lone individual, enabling more time to forage (Gartlan & Struhsaker, 1972; Struhsaker, 1981; Pook & Pook, 1982; Gautier-Hion et al., 1983; Roberts, 1996; Hardie & Buchanan-Smith, 1997). Indeed a study specifically looking at the difference in the rate of vigilance between single- and mixed-species captive troops of tamarins (*Saguinus fuscicollis* and *S. labiatus*), found that the mean time each individual spent in vigilance was less in mixed-species groups (Hardie & Buchanan-Smith, 1997). Though it must be noted that group vigilance is not always equally distributed among group members, with some individuals or species spending less time being vigilant or less active during group defence (e.g. Bertram, 1980; Pullium, Pyke & Caraco, 1982; Childress & Lung, 2003).

In addition to having more 'ears and eyes', the presence of another species and the increased number of individuals in mixed-species groups can lead to 'predator confusion' in an attack situation; due to the unpredictable, evasive movements (fleeing with intersecting pathways) of mixed-species prey, which makes it more difficult for predators to single out any one individual (Curio, 1976; Struhsaker, 1981; Landeau & Terborgh, 1986; Stensland et al., 2003). Though it must be noted that prey animals themselves may also become confused, becoming separated, or colliding with another individual, both impeding their escape and potentially making them more susceptible to predation. Furthermore, group membership is not always a guarantee of safety from predation, as individuals are seldom equally at risk (some will be disproportionately chosen), thus the position of an individual within a group (e.g. central vs peripheral) can also affect the probability of being preyed upon (Hamilton, 1971; Robinson, 1981; Krause, 1994; Lee, 1994; Morrell, Ruxton & James, 2011). Mixed-species groups could also be acting as 'selfish-herds' (i.e. prey individuals try to position another prey individual between themselves and a predator), whereby dominant individuals/species place themselves in positions near to the center of the group, gaining an increased measure of safety from lower ranking individuals/species on the periphery (using them as living shields - Hamilton, 1971; Terborgh, 1990). For example, in mixed-species observations of red colobus (*Piliocolobus badius* – formerly *Colobus badius*) and Diana monkeys (*Cercopithecus diana*), Holenweg, Noë and Schabel (1996) suggest that each species benefits from the difference in vertical stratification. The arboreal *P. badius* use the terrestrial *C. diana* as a shield against predatory chimpanzees (*Pan troglodytes*) attacking from below; and in turn *C. diana* use *P. badius* as a shield against potential aerial predators such as the crowned eagle (*Stephanoaetus coronatus*).

Similarly, larger mixed-species groups may 'dilute' the success of a predatory attack, in that through there being more individuals present, it is statistically less likely for an individual to become the unfortunate victim of attack, so long as they share a common predator (i.e. safety in numbers – see Curio, 1976; Bertram, 1978; Foster & Treherne, 1981; Terborgh, 1986, 1990; Turner & Pitcher, 1986; Waser, 1987; Delm, 1990; Fitzgibbon, 1990, 1994; Roberts, 1996; Schmitt, Stears, Wilmers & Shrader, 2014; Lehtonen & Jaatinen, 2016; Goodale et al., 2017). If prey individuals share a common predator and are all capable of taking evasive action in the event of an attack, where a predator can only kill one prey individual per successful attack, then the probability that any particular individual is the target victim is $\frac{1}{N}$ where N is the number of individuals in the group (Terborgh, 1990). Thus, as N increases the derived benefit of reduced predation risk also increases. To some extent the dilution effect may be offset by increased conspicuousness from being in larger (more detectable) groups, compared to solitary individuals that are better able to escape detection (e.g. through crypsis), however the benefit of the increased collective ability of larger groups to detect a predator will likely exceed the disadvantage (Vine, 1971; Treisman, 1975a, 1975b; Stensland et al., 2003; Goodale et al., 2017). Finally, it is worth noting that not all prey animals will flee from potential predators, for instance individuals living in large groups (single- or mixed-species) will generally be able to defend themselves more effectively than solitary individuals (Gautier-Hion & Tutin, 1988; Stensland et al., 2003). Indeed, cooperative group defense against predators (e.g. mobbing) has been reported quite often in the primate literature (e.g. Coss & Owings, 1977; Busse, 1980; Chapman, 1986; Bartecki & Heymann, 1987; Boinski, 1988b; Buchanan-Smith, 1990; Ferrari & Lopes Ferrari, 1990; Heymann, 1990b; Pettifor, 1990; Ross, 1993; Iwamoto, Mori, Kawai, Bekele, 1996; Boesch & Boesch-Achermann, 2000; Tello, Huck & Heymann, 2002; Perry, Manson, Dower & Wikberg, 2003).

Living in groups therefore has the potential of dual benefits – both increased foraging efficiency and decreased predation risk. This is what Pulliam et al. (1982) called "the double benefit of grouping" and it has the potential to apply to mixed-species groups as much as to single-species groups. However, regardless of the benefits, we still need to examine how mixed-species group are defined.

1.4 Defining mixed-species groups

As previously noted, animal groups that contain multiple species have been referred to in the literature in a number of ways, such as: multispecies groups (Wing, 1946); mixed groups (Eaton, 1953); interspecific groups (Rice, 1956); polyspecific associations (Gartlan & Struhsaker, 1972) or; mixed-species associations (Powell, 1985). Often these terms are considered to mean the same thing, with group and association being used interchangeably, however as will be discussed further in this section there are differences between an association and a group. In the existing literature a clear definition of a mixed-species group is either lacking or tends to be very broad, which makes it difficult to compare between studies. Some recent attempts have been made to distinguish between the different terminologies, for instance an extensive review on mixed-species groups in mammals by Stensland et al. (2003, p.206) provides the following: *"our definition of interspecific or mixed species group is restricted to groups that are a result of attraction between participants themselves and not due to aggregation around clumped resources"*. The authors go on to clarify that attraction should be regarded as either mutual or single, so long as the presence of the other species is tolerated by the non-attracted species; and they also note that it may be difficult to distinguish between a mixed-species group and an aggregation. However, the main point of focus in Stensland et al.'s (2003) definition is that mixed-species groups will occur irrespective of concentrated resources, which should help to differentiate aggregations. Still, I find that this definition is somewhat lacking, as it does not include any of the prerequisites for animal groupings that were mentioned in section 1.1.

Goodale et al. (2017, p. 3) have also attempted to provide a definition for mixed-species groups (MSG) based on work by Viscido and Shrestha (2015) *"an MSG includes individuals that (1) are in spatial proximity to each other, but move separately in the same direction, and (2) interact with each other, with this interaction being more critical for the formation and maintenance of the group than external factors, such as resource patches that structure aggregations"*. Furthermore, they provide a glossary in an attempt to make the distinctions between the different terminologies used (e.g. aggregation and mixed-species association) clearer (see Table 1.2).

Table 1.2 *Summary of the definitions of terms used in studies on mixed-species animal groups (adapted from Goodale et al., 2017, p. 2).*

Term	**Definition**
Aggregation	A gathering of animals around a resource (e.g. feeding tree or watering hole) or a specific location
Association	A gathering of individual animals that belong to the same trophic level and is not as persistent as symbiosis (i.e. parasite-host), as individuals will frequently join and leave
Group	A group of independently* moving animals from more than one species found in close proximity, which interact with one another

*moving separately rather than on or inside each other

While their definition for mixed-species groups (Goodale et al., 2017) does include some of the prerequisites for grouping (see Section 1.1) that relate to proximity and interactions, there is still some ambiguity and overlap. For instance, according to the glossary of terms (see Goodale et al., 2017) the main difference between a mixed-species association and group is that in an association, individuals will frequently join and leave, and in a group, individuals are in close proximity and interact with each other (Table 1.2). There are a number of issues with this; (1) depending on the species involved, mixed-species groups often vary in their duration (e.g. minutes, hours, years), frequency (e.g. daily, seasonally) and structure, with individuals frequently joining and leaving (see Cords, 1987); (2) close proximity as a proxy for grouping will differ between species and furthermore it disregards more complex group structures such as fission-fusion societies, and animals that are able to communicate acoustically across large distances (see Section 1.1). In fact, if I were to apply Goodale et al.'s (2017) definition to previous literature on mixed-species groups, the majority of them would be classed as either an aggregation or association. While it may be more appropriate in some instances to use the term association rather than group, it would still be difficult to apply their definition across all taxa, especially given the vast complexity in the different modes and environments (e.g. dense forest vs. open savannah and coral reefs vs. open water) in which animals live.

Therefore, as with single-species animal grouping behaviour, rather than attempting to find an all-encompassing definition of a mixed-species group, it would be more prudent to develop more operational definitions (see Section 1.1), in conjunction with methodologies where the "groupness" of mixed-species groups can be tested and quantified. Figure 1.1

outlines the methods used in this thesis that test the prerequisites for grouping. The stability and socialness of groups were tested using social network analysis, and proximity and behavioural coordination in time and space were tested separately; proximity - examining group spread, and coordination – examining behavioural synchrony (see Figure 1.1 and Section 1.1).

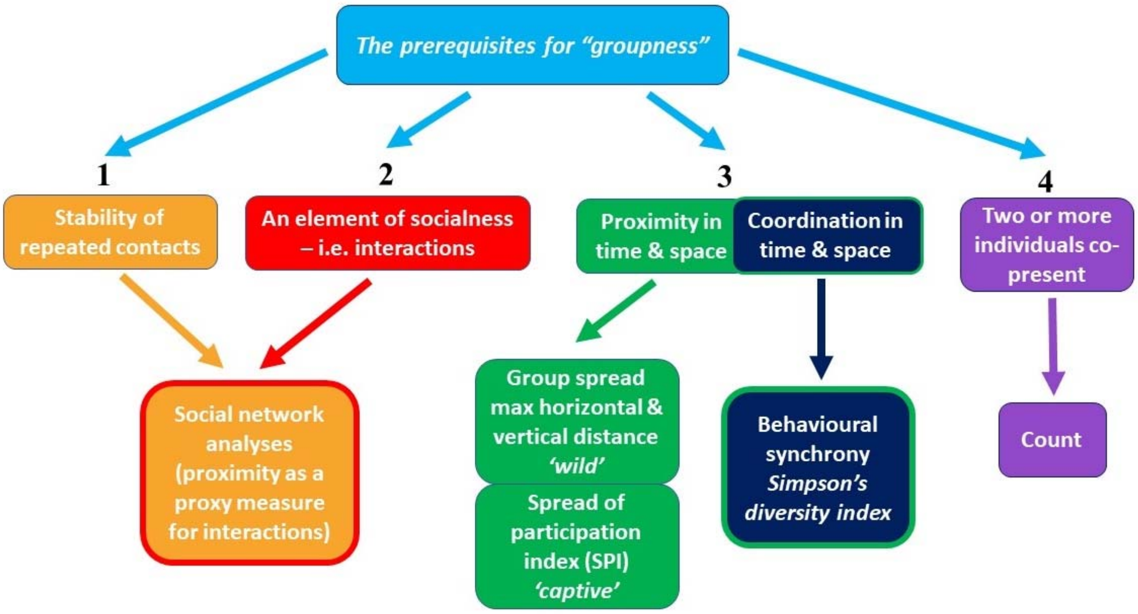

Figure 1.1 Schematic illustration of the methods that will be used in this thesis to examine whether *Sapajus* and *Saimiri* live in mixed-species groups. Prerequisites (1) and (2) are investigated in Chapter 6, and prerequisite (3) is investigated in Chapters 2, 4 and 5. Prerequisite (4) was not specifically tested but was a necessary requirement.

1.4.1 Mixed-species groups in the primate literature

Mixed-species groups have been described in a number of different species, but the most detailed behavioural studies are generally found within the primate literature (see review in Stensland et al., 2003). Mixed-species groups between two or more primate species have been described in forests of the Paleotropics (e.g. Africa: Gartlan & Struhsaker, 1972; Gautier-Hion & Gautier, 1974; Waser, 1980; Struhsaker, 1981; Cords, 1990a; Noë & Bshary, 1997; Buzzard, 2010; and Asia: Rodman, 1978; Southwick & Southwick, 1983) and the Neotropics (e.g. South America: Klein & Klein, 1973; Fleagle, Mittermeier & Skopec, 1981; Pook & Pook, 1982; Terborgh, 1983; Podolsky, 1990; Peres, 1992; 1993a, 1993b; Buchanan-Smith, 1999a; Heyman & Buchanan-Smith, 2000; Smith, Buchanan-Smith, Surridge & Mundy, 2005; Pinheiro, Ferrari & Lopes, 2011). One common feature is that the species that tend to form mixed-species groups are small to medium sized, diurnal, frugivorous or omnivorous, and are often similar in terms of their ecology, behaviour, and physicality (Gartlan & Struhsaker, 1972; Cords, 1987; Peres, 1992).

In general, two or more species are considered to be in a group or forming associations when individuals of the different species are 'spatially intermingled', which usually means that they are in either the same or neighbouring trees and within a certain (proximal) distance, such as ≤20m, ≤50m or ≤100yds (e.g. Klein & Klein, 1973; Struhsaker, 1981; Terborgh, 1983; Whitesides, 1989; Podolsky, 1990), and in captivity individuals need to be in the same enclosure and ≤50cm (e.g. Leonardi, Buchanan-Smith, Dufour, MacDonald & Whiten, 2010; Buchanan-Smith, Griciute, Daoudi Leonardi & Whiten, 2013). Another way to determine whether two species are forming a mixed-species group is to test whether or not they occur by chance, due to moving around independently. Waser (1982, 1984) examined this through a perfect gas model, in order to test whether the association rate between two species was greater than expected by chance (Waser's gas model). The advantage of the gas model is that in addition to the prediction of time spent in association, it can also generate expected encounter rates and expected mean duration of association between the two species being observed. However, one of the drawbacks of this model is the assumption that all groups use all parts of their home range equally, and in most cases this assumption is violated, as some individuals may either frequently visit or avoid certain areas in their home range more than others (Holenweg et al., 1996).

The duration and stability of primate mixed-species groups vary considerably, from ephemeral encounters in fruiting trees (e.g. Gartlan & Struhsaker, 1972; Mittermeier & van Roosmalen, 1981; Struhsaker, 1981; Waser, 1982; Whitesides, 1989) to almost permanent membership (e.g. Gautier-Hion & Gautier, 1974; Terborgh, 1983; Peres, 1992; Buchanan-Smith, 1990; 1999), with long-term grouping/associations occurring mostly in species of the same genera. For example, a mixed-species group of saddle-backed tamarins (*Saguinus fuscicollis*) and emperor tamarins (*S. imperator*) were reported to have been associating for approximately three years (Terborgh, 1983). Similarly, mixed-species groups between *S. fuscicollis* and *S. mystax* (moustached tamarin) were reported to spend between 72% and 98% of their daily activity period together (Heymann, 1990a; Peres, 1992; Smith, 1997). Whereas studies on mixed-species groups of guenons (*Cercopithecus* spp.) have reported durations to last from short aggregations at common resources (e.g. Oates & Whitesides, 1990; Whitesides, 1989), to semi-permanent and seasonal groupings (e.g. Cords, 1987; Mitani, 1991; Struhsaker, 1981), to near constant association (97% of observation time) (e.g. Gautier-Hion et al., 1983). These differences in duration/stability may be attributed to differences in ecological conditions, as not all populations of the same species are necessarily found in similar mixed groups (Whitesides, 1989; Cords, 1990b; Podolsky, 1990; Goodale et al., 2017). If the species are ecologically similar then competition is likely to increase, but if their needs are too different then the advantage of staying together decrease (Heymann, 1997). Alternatively, ecologically different species may gain advantages for different reasons, for example while one species gains foraging advantages, the other may benefit from reduced risk of predation (e.g. Terborgh, 1983; Heymann & Buchanan-Smith, 2000).

While mixed-species groups comprised of primates from different genera are less common, they do occur. For instance, colobines have been found to group with cercopithecines at various sites in Africa (e.g. Oates & Whitesides, 1990; McGraw, 1994; Chapman & Chapman, 2000a; Teelen, 2007). One study found that red-tailed monkeys (*Cercopithcus ascanius*) actively initiated, maintained and terminated groupings with red colobus (*Piliocolobus ruomitratus*), with the main reason for grouping, to take advantage of the vigilance of the latter from predators such as raptors and chimpanzees (*Pan troglodytes*) (Teelen, 2007). Another notable example is mixed-species groups of tufted capuchins (*Sapajus* spp.) and squirrel monkeys (*Saimiri* spp.) (e.g. Klein & Klein, 1973; Baldwin & Baldwin, 1971, 1981; Fleagle et al., 1981; Terborgh, 1983; Podolsky, 1990; Pinheiro, Ferrari & Lopes, 2011; Levi, Silvius, Oliveira, Cummings & Fragoso, 2013; Frechette, Sieving & Boinski, 2014 – also see Table 1.5). It should be noted that both *Sapajus* spp. and *Saimiri* spp. have also been reported in associations with other monkeys, though often less systematically, and the frequency and duration of encounters are lower than that of *Sapajus*-*Saimiri* sightings. For *Saimiri* spp. these include: howler monkeys (*Alouatta* sp.), titi monkeys (*Callicebus* sp.), tamarins (*Saguinus* sp.), uakaris (*Cacajao* sp.). sakis (*Pithecia* sp.), bearded sakis (*Chiropotes* sp.), white-fronted capuchins (*Cebus albifrons*) and spider monkeys (*Ateles* sp.) (e.g. Terborgh, 1983; Pinheiro et al., 2011), and for *Sapajus* spp. these include: bearded sakis (*Chiropotes* sp.), howler monkeys (*Alouatta* sp.) and spider monkeys (*Ateles* sp.) (e.g. Mittermeier & van Roosmalen, 1981; Terborgh, 1983).

Observations of *Sapajus* spp. and *Saimiri* spp. mixed-species groups are often described as being temporary (lasting anything from a few hours up to around ten days - see Table 1.5) compared to mixed-species groups of tamarins, which are much longer lasting (e.g. Pook & Pook, 1982; Terborgh, 1983; Buchanan-Smith, 1990). Additionally the criteria provided for grouping varies between studies, with some stating the monkeys need to be in close proximity (i.e. distance not specified, <20m or <50m – see Table 1.5), further emphasising the inconsistency in how mixed-species groups are defined. Mixed-species group formation is presumed to be favoured due to their dietary overlap and having some shared predators (e.g. raptors and snakes) (Terborgh, 1983; Podolsky, 1990). Interestingly, this does not appear to be the case for all areas inhabited by capuchin and squirrel monkeys, Boinski (1989) reported that despite having overlapping territories, mixed-species observations of *Saimiri oerstedii* and *Cebus capucinus* were minimal, and even when the two species were observed together (<50m), there was little evidence to suggest that either was benefitting from the association. It could therefore be argued that the capuchin-squirrel monkey association is not species specific, but rather due to whether the benefits of the association outweigh the costs in relation to the geographical and ecological factors presenting the opportunity for this (Boinski, 1989).

For this thesis, I conducted a series of observational studies on Guianan brown capuchins (*Sapajus apella*) and Guianan squirrel monkeys (*Saimiri sciureus*), to test more operational definitions of animal groups. I used different methodological approaches to quantify 'groupness' in mixed-species groups, specifically testing two of the prerequisites required for grouping (i.e. an element of socialness and proximity and behavioural coordination in time and space - see Section 1.1; Figure 1.1), and touching on stability by exploring the repeated nature of relationships, based on proximity between individuals. These studies will help to produce a more complete picture of how we can measure the groupness of animals in order to determine whether they are behaving as a true mixed-species group or not (e.g. could be a mixed-species association or aggregation). I describe each of the chapters in more detail after the section on the study species.

PART II: STUDY GENERA & STUDY SPECIES

1.5 Taxonomy & distribution

Capuchin (*Cebus* spp. and *Sapajus* spp.) and squirrel monkeys are both Neotropical[1] primates (Platyrrhini) that are found throughout much of Central and South America. However, their exact placement within the taxonomic classification systems, has come under much debate over the years. For instance, the family Cebidae was previously a catch-all for any Neotropical primates that were not marmosets or tamarins as exemplified by Hill (1960, 1962) and Hershkowitz (1977). However, a revision of the higher taxonomy by Rosenberger (1980, 1981) redefined the Cebidae based on a number of morphological differences as comprising two subfamilies: (1) Callitrichinae (marmosets, lion tamarins, tamarins and Goeldi's monkey) and; (2) Cebinae (capuchin and squirrel monkeys), which are still broadly accepted today. His arrangement was adopted by Groves (2001), but under three subfamilies: (1) Hapalinae (Callitrichinae); (2) Cebinae and (3) Chrysotrichinae (Saimiriinae) and by Rylands and Mittermeier (2013) where they are again considered as two distinct families (Callitrichidae and Cebidae), with squirrel monkeys (subfamily Saimiriinae, genus = *Saimiri*) and capuchins (subfamily Cebinae, genera *Cebus* and *Sapajus*), comprising a monophyletic clade that make up Cebidae (see also Jack, 2011 for a discussion of the phylogenetic debate).

In addition to this, the detailed taxonomy of the capuchin and squirrel monkeys has undergone much investigation and reclassification. The capuchins were previously all grouped under the same genus (*Cebus*) with four recognised species: *C. apella, C. capucinus, C. albifrons* and *C. olivaceus*, and more than 30 subspecies traditionally recognised (see review in Jack, 2011). There is still some contention as to whether a further four (*C. kaapori, C. libidinosus, C. xanthosternos, and C. nigritus*) should be recognised as distinct species rather than subspecies of *C. apella* (Rylands et al., 2000; Groves, 2001; Fragaszy, Visalberghi & Fedigan, 2004; Jack, 2011). The four 'recognised' species were divided into two main groups based on differences in cranial morphology (Hershkowitz, 1949): the robust/tufted (*C. apella*) and gracile/untufted (*C. albifrons, C. capucinus, and C. olivaceus*). All major revisions over the past ~50 years have maintained this division. However extensive research by Silva (2001) and Lynch Alfaro, Silva & Rylands (2012a) and Lynch Alfaro et al. (2012b) suggest that based on the differences in cranial morphology

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[1] This nomenclature along with 'new world' is widely used within the literature, however, more recently (i.e. after the Black Lives Matter protests of 2020) it has come under question; as part of de-colonising primatology alternatives include Pan-American or Platyrrhine, which I will endevor to apply in future.

(e.g. robust: presence of sagittal crest, browridge extends into forehead, robust mandible; gracile: no sagittal crest, horizontal browridge, less robust mandible), behaviour and geographical distribution of the robust and gracile capuchins should be classified as distinct genera: *Sapajus* and *Cebus* respectively. There are currently 8 recognised *Sapajus* species and ~3 subspecies, and 11 *Cebus species*, and ~8 subspecies (see Rylands & Mittermeier, 2013 and Table 1.3).

Table 1.3 *Capuchin taxonomy including current recognised species of* Sapajus *and* Cebus *according to Rylands and Mittermeier (2013). (N=north, S=south, E=east, W=west and C=central).*

Common Name	**Latin Name**	**Distribution**
Robust/tufted capuchins genera *Sapajus*		
Black-horned capuchin	*Sapajus nigritus*	NE Argentina, SE Brazil
Hooded capuchin	*Sapajus cay*	SE Bolivia, N Argentina, Brazil, Paraguay
Crested capuchin	*Sapajus robustus*	SE Brazil
Bearded capuchin	*Sapajus libidinosus*	CN East Brazil
Yellow-breasted capuchin	*Sapajus xanthosternos*	EC Brazil
Blond-capuchin	*Sapajus flavius*	Coastal NE Brazil
Guianan brown capuchin	*Sapajus apella*	Guianas and N Brazil
Large-headed capuchin	*Sapajus macrocephalus*	E Colombia, Venezuela, E Ecaudor, E Peru, W Brazil, CN Bolivia
Gracile/untufted capuchins genera *Cebus*		
Marañón white-fronted capuchin	*Cebus yuracus*	S Colombia, E Ecuador, NE Peru
Shock-headed capuchin	*Cebus cuscinus*	SE Peru, NW Bolivia
Spix's white-fronted capuchin	*Cebus unicolor*	Brazil, E Peru, N Bolivia
Humboldt's white-fronted capuchin	*Cebus albifrons*	S Venezuela, S&E Colombia, NW Brazil
Guianan weeper capuchin	*Cebus olivaceus*	Guianas
Ka'apor capuchin	*Cebus kaapori*	NE Brazil
Venezuelan brown capuchin	*Cebus brunneus*	N Venezuela
Sierra de Perijá white-fronted Capuchin	*Cebus leucocephalus*	N Colombia
Río Cesar white-fronted capuchin	*Cebus cesarae*	N Colombia
Varied white-fronted capuchin	*Cebus versicolor*	N Colombia
Colombian white-throated capuchin	*Cebus capucinus*	W Colombia, NW Ecuador
Ecuadorian white-fronted capuchin	*Cebus aequatorialis*	Ecuador, NW Peru
Panamanian white-faced capuchin	*Cebus imitator*	N Honduras, C & W Nicaragua, Costa Rica, W Panama

As a result of the evidence provided by Silva (2001) and Lynch Alfaro et al. (2012a, 2012b), in this thesis I will adopt their classification of the capuchins. For further clarification, when describing or referring to previously published data (which use *Cebus* instead of *Sapajus*), for consistency I will (where possible) refer to the species of capuchin monkey using the updated nomenclature (for further discussion of the taxonomy of capuchin monkeys see – Janson & Boinski, 1992; Sussman, 2000, 2003; Rylands et al., 2000; Fragaszy et al., 2004; Lynch Alfaro et al., 2012a, 2012b; Rylands & Mittermeier, 2013; Lima et al., 2017).

The taxonomy of squirrel monkeys has likewise been subject to extensive debate and re-analysis, resulting in classifications of just one species to as many as seven species and 17 subspecies (see Rylands & Mittermeier, 2013), though unlike the capuchins they remain classified under the same genus '*Saimiri*'. Historically, *Saimiri* spp. were divided into two groups based on the shape of the white brow-line above the eyes, which was either narrow and rounded like a Roman arch, or more pointed like a Gothic arch (Hershkowitz, 1984; Kinzey, 1997). Costello, Dickinson, Rosenberger, Boinski and Szalay (1993) reviewed geographic difference in pelage colouration, cranial and dental morphology, karyology, biochemistry and behaviour of *Saimiri* spp. and concluded that there were greater differences between the Central and South American *Saimiri* spp. than between the Southern groups. Based on these differences just two species were recognised: the Central American *Saimiri oerstedii* and the South American *S. sciureus*, then three species were later recognised including *S. boliviensis* (Costello et al., 1993; Sussman, 2000, 2003) and then a further two *S. ustus* and *S. vanzolinii* (see Boinski, 1999; Jack, 2011; Zimbler-DeLorenzo & Stone, 2011), and now there are seven separate species (see Table 1.4) of *Saimiri* with ~7 subspecies (see Rylands & Mittermeier, 2013; Lynch-Alfaro et al., 2015). In a similar way to much of the earlier research on tufted capuchins (i.e. referring to all as *Cebus apella*), much of the early publications on South American squirrel monkeys refer to them as *Saimiri sciureus.* Therefore, in order to avoid any misapprehension regarding the taxonomy of both capuchin and squirrel monkeys, only the most recent reclassifications will be used when referring to previous studies.

The geographic distribution of capuchins and squirrel monkeys covers much of Central and South America, with extensive overlaps between the three genera (Baldwin & Baldwin, 1981; Klein & Klein, 1973; Fleagle & Mittermeier, 1980; Fleagle, Mittermeier & Skopec, 1981; Terborgh, 1983; Podolsky, 1990; Kinzey, 1997a, 1997b; Boinski, 1999; Groves, 2001; Sussman, 2003; Fragazy et al., 2004; Zimbler-DeLorenzo & Stone, 2011; Lynch Alfaro et al., 2012a, 2012b; Rylands & Mittermeier, 2013; Frechette et al., 2014 – see also Tables 1.3, 1.4). They occupy many different types of forest including mangrove, humid and dry lowland and submontane, cloud, seasonally flooded, swamp and secondary. This broad distribution of the monkeys is likely due to their varied (omnivorous) and flexible diets (e.g. squirrel monkeys become more insectivorous in times of fruit scarcity), and their ability to adapt, manipulate their environment (e.g. tool use in *Sapajus* – see Visalberghi, 1987; Langguth & Alonso, 1997; Boinski, Quatrone & Swartz, 2000; Moura & Lee, 2004; Canale, Guidorizzi, Kierulff & Gatto, 2009) and exploit resources in a variety of different environments (Freese & Oppenheimer, 1981; Kinzey, 1997a, 1997b; Boinski, 1999, 2002; Sussman, 2003; Fragaszy et al., 2004; Jack, 2011; Rylands & Mittermeier, 2013).

Table 1.4 *Squirrel monkey taxonomy and distribution of recognised species according to Rylands and Mittermeier (2013). (N=north, S=south, E=east, W=west and C=central).*

Common Name	**Latin Name**	**Distribution**
Central American squirrel monkey	*Saimiri oerstedii*	SE Costa Rica, SW Panama
Humboldt's squirrel monkey	*Saimiri cassiquiarensis*	Colombian & Brazilian Amazon, S Venezuela
Ecuadorian squirrel monkey	*Saimiri macrodon*	W Brazilian Amazon, S Colombia, E Ecuador, N & E Peru
Golden-backed squirrel monkey	*Saimiri ustus*	Brazilian Amazon
Guianan squirrel monkey	*Saimiri sciureus*	Guianas and N Brazil
Black-capped squirrel monkey	*Saimiri boliviensis*	Upper Brazilian Amazon, N Bolivia, N & C Peru
Black-headed squirrel monkey	*Saimiri vanzolinii*	Brazilian Amazon

1.6 Capuchin-squirrel monkey mixed-species groups

Of the Neotropical primates known to form mixed-species groups, the most commonly reported within the literature is that between the capuchin and squirrel monkeys (Thorington, 1967; Baldwin & Baldwin, 1971, 1981; Klein & Klein, 1973; Fleagle et al., 1981; Terborgh, 1983; Podolsky, 1990; Kinzey, 1997a, 1997b; Boinski, 1999; Sussman, 2000, 2003; Pinherio et al., 2011 – see also Table 1.5). The most well studied groupings are *Saimiri sciureus* with *Sapajus apella* (e.g. Fleagle et al., 1981; Mittermeier & van Roosmalen, 1981; Boinski 1999) in Suriname, and *Saimiri boliviensis* with *Sapajus macrocephallus* and *Cebus* *yuracus* (Terborgh, 1983; Podolsky, 1990) in Peru. As noted earlier, capuchins and squirrel monkeys have also been observed in mixed-species groupings with other primate species, and not all capuchin-squirrel monkey species combinations form mixed-species groups (see Section 1.4.1). The Central American *Saimiri oerstedii* and *Cebus imitator* were rarely observed in mixed-species groupings (<50m) and there was little to no evidence that supports the double benefit of grouping hypothesis (Pulliam et al., 1982; Boinski, 1989; Zimbler-DeLorenzo & Stone, 2011). Boinski (1989) suggests that the lack of mixed-species grouping is due to a combination of the high foraging costs of mixing and limited benefits associated with predator directed vigilance (i.e. the majority of *C. imitator* vigilance is directed at other conspecific males). It could therefore be argued that in order for capuchins and squirrel monkeys to form mixed-species groups not only do the benefits of grouping together need to outweigh the costs, but the geographical location (i.e. Central or South America) and habitat need to allow for the opportunity to mix (Boinski, 1989).

Therefore, it can perhaps be inferred that the environments of *Sapajus* and *Saimiri* in South America are more conducive to the ‘double benefits’ (Pulliam et al., 1982) of forming mixed-species groups than in Central America (e.g. Terborgh, 1983; Huntingford, 1984; Boinski, 1989; Heymann & Smith, 2000; Stensland et al., 2013; see Table 1.5). Some authors argue that *Saimiri* spp. benefit more from the association by taking advantage of the extractive foraging techniques of capuchins (*Cebus* spp./*Sapajus* spp.); they are messy eaters and often discard half-eaten fruits and nuts that *Saimiri* spp. may not otherwise be able to access (e.g. Terborgh, 1983; Podolsky, 1990). Furthermore, capuchins generally occupy higher sections of the canopy compared to *Saimiri* (e.g. Fleagle et al., 1981) and this combined with the rapid movements of *Cebus* spp./*Sapajus* spp. while locomoting, may increase the prey capture rates of *Saimiri* spp. by feeding on insects that are flushed from their hiding places (e.g. Gartlan & Struhsaker, 1972; Klein & Klein, 1973; Waser, 1982). A study by Peres (1992) observed similar behaviour in mixed-species groups of tamarins, where *Saguinus mystax* (higher in the canopy) flushed out insects to lower substrates, facilitating capture by *S. fuscicollis* (lower in the canopy).

Saimiri spp. can also benefit from parasitism of knowledge (eavesdropping) of *Cebus* spp./*Sapajus* spp. to locate foraging sites (i.e. fruiting trees). For example, Terborgh (1983)

Table 1.5 *Previous research on mixed-species groups of* Sapajus *spp. (formerly* Cebus *– see Lynch Alfaro, Silva & Rylands, 2012a) and* Saimiri *spp. Sections with N/A are for details not included in the journal article, or unable to access information due to publication/access restrictions.*

Species & Site	Group size & no. groups	Home Range / Transect size / Enclosure size	Duration of study	Frequency &/or duration of associations	Distance criterion for group & rationale	Source
Field studies						
S. sciureus and *S. apella apella* **Hacienda Barbascal, Monte Seco, Colombian Llanos**	*Sapajus n*~7 *Saimiri n*~18	750yds x 250yds	~2 months	N/A	No specific distance criterion provided for mixed-species Foraging/ antipredator	Thorington, 1967
S. sciureus and *S. apella* **Panama, Colombia, Brazil & Peru**	*Saimiri* Panama & Colombia: *n*~10-35 Brazil: ~200-300 Peru: *n*~150-300 *Sapajus*=N/A	Panama ~50 acres Colombia unspecified Brazil unspecified Peru unspecified (maps provided in journal)	Panama: 1 month Colombia, Brazil & Peru: ~4 months	Least observations in Panama 30% of *Saimiri* troops observed near *Sapajus* in Colombia Peru 1.2 hours Brazil x2 *Sapajus* associated consistently with a subgroup of 60-80 *Saimiri*	No specific distance criterion provided for mixed-species Foraging	Baldwin & Baldwin, 1971
S. sciureus and *S. apella apella* **La Macarena, Colombia**	*Sapajus n*=2-12 *Saimiri n*=25-30	3 square mile study site	19 months	Observed together *n*=119 (more than single-species) maximum 2 hours.	Close spatial proximity – in mixed bands or within 100 yards (~91m)	Klein & Klein, 1973
S. sciureus and *S. apella* **Raleighvallen-Voltzberg Nature Reserve, Central Suriname**	N/A	N/A	4 months (wet season)	29 mixed observations from 50 *Sapajus* and 30 *Saimiri* observations	No specific distance criterion provided for mixed-species Foraging	Fleagle, Mittermeier & Skopec, 1981
S. sciureus, Sapajus apella and *Cebus unicolor* **Manu National Park, Peru**	*Sapajus n*=11-16 (7-10 troops) *Saimiri n*=35 ±5 (4-5 troops)	*S. apella* 80 (ha) *S. sciureus* >250 (ha)	12 months	A few hours or as long as 10 days	Group/association <50m Foraging/antipredator	Terborgh, 1983
S. sciureus and *S. apella* **Manu National Park, Peru**	*Sapajus n*=10-12 (3 troops) *Saimiri n*=40-50 (1 focal troop)	*S. sciureus* 400 (ha) *S. apella* ~80 (ha)	4 months (dry season)	50.2% of observations (association bouts between 5-12 days)	Group/association <20m Foraging	Podolsky, 1990

Table 1.5 *continued.*

Species & Site	Group size & no. groups	Home Range / Transect size / Enclosure size	Duration of study	Frequency &/or duration of associations	Distance criterion for association & rationale	Source
Field studies continued						
S. sciureus, S. apella, Chiropotes sp. *Alouatta belzebul, Saguinus niger, Aotus azarae, Callicebus moloch* **Tucuruı´ reservoir - Southeastern Para´, Brazil**	*S. sciureus n*=30-39 (2 troops) *S. apella* unknown	*S. sciureus* 75-77.5 (ha) *S. apella* unknown but sympatric with *S. sciureus*	6 months (wet & dry seasons)	Troop B4 100% of observations (*n*=1309) Troop IG 54.8% of observations (*n*=1148)	Group/association <50m Foraging/antipredator	Pinheiro, Ferrari & Lopes, 2011
S. sciureus, *S. apella* and *C. olivaceus* **Guyanas**	Unknown (refers to density estimates and abundance)	94 transects covering 48,000km^2	3 years May 2007 - June 2010	N/A (*Saimiri* rarely observed without *Sapajus)*	No specific distance criterion provided for mixed-species Foraging	Levi et al., 2013
S. sciureus and *S. apella* **Raleighvallen-Voltzberg Nature Reserve, Central Suriname**	*S. sciureus n=25*-28 (2 troops) *S. apella* unknown	1.6 million (ha) - Liana/low forest 40%; High/primary forest 40%; Swamp forest 10%; Bamboo patches 10%	3 years January 1998 - May 2001	*S. sciureus* 52% of time in mixed-species groups with *S. apella*.	Group/association <50m Antipredator	Frechette, Sieving & Boinski, 2014
Captive studies						
Saimiri sp. S. apella, *Ateles geoffroyi, Myrmacophagia trydactyla, Tapirus terrestris* and a variety of bird species. **Chicago Zoological Park**	*Saimiri* sp. *n*=10-22 *S. apella n*=9-14	~ 22.9m x 22.9m x 21.3m	1984-1999 (review)	N/A	N/A noted juvenile *Saimiri* would sit in laps of juvenile *Sapajus* and engage in play	Sodaro, 1999
S. sciureus and *S. apella* **Living Links, Edinburgh Zoo**	*S. sciureus n*=10-15 (2 troops) *S. apella n*=5-7 (2 troops)	*Saimiri* indoor: 5.5m x 4.5m x 6m *Sapajus* indoor: 7m x 4.5m x 6m shared outdoor: 900m^2	2 months July-August 2008	39hr obs = 96 interactions recorded (2.5 interactions/hr)	Group/association <50cm Social enrichment	Leonardi et al., 2010
S. sciureus and *S. apella* **Living Links, Edinburgh Zoo**	*S. sciureus n*=10-17 (2 troops) *S. apella n*=6-9 (2 troops)	*Saimiri* indoor: 5.5m x 4.5m x 6m *Sapajus* indoor: 7m x 4.5m x 6m shared outdoor: 900m^2	6 months July-August 2008, 2009 & 2010	Over 3 years spent 80% of time in shared enclosures	Group/association <50cm Social enrichment	Buchanan-Smith et al., 2013

observed that one troop of *S. boliviensis* (whose home range was larger than *C. aequatorialis* and *S. macrocephalus*) would join multiple troops of *C. aequatorialis* and *S. macrocephalus* (whose home ranges were smaller; more knowledgeable of a smaller area), but it was also noted that during periods of food scarcity, *C. aequatorialis* and *S. macrocephalus* were able to take advantage of *S. bolivensis'* knowledge by following them to food sources. In addition to foraging benefits, *Saimiri* spp. also benefit from *Cebus* spp./*Sapajus* spp. alarm calls, indeed *Saimiri* spp. have been observed to respond more readily to *Cebus* spp./*Sapajus* spp. alarm calls than they do the alarm calls of conspecifics (Terborgh, 1983).

1.7 General characteristics

It is important to understand the general characteristics of a species if we are to understand the selection pressures and potential benefits on the formation of groups. For example, size differential (i.e. if differ in body size by at least 8%) has been shown to be directly associated with duration and stability in *Saguinus* spp. mixed-species groups, in addition to niche differentiation (e.g. Heymann, 1997). Similar findings are noted in the literature on *Cebus* spp./*Sapajus* spp. and *Saimiri* spp. mixed-species groups (e.g. Terborgh, 1983; Podolsky, 1990). *Cebus* spp./*Sapajus* spp. are medium sized primates, and are sexually dimorphic, with males typically being larger, weighing 19.5%-27% (~1.3-4.8kg, $\bar{x}$=3.0kg) more than females (~1.4-3.4kg, $\bar{x}$=2.3kg), and have larger canine teeth (16-22%) than females (e.g. Kay, Plavcan, Glander & Wright, 1988; see also review in Jack, 2011). *Saimiri* spp. are considerably much smaller than *Cebus* spp./*Sapajus* spp. especially when compared to other primate species that form mixed-species groups such as tamarins (e.g. Terborgh, 1983; Buchanan-Smith, 1990) and guenons (e.g. Cords, 1990a). However, the degree of sexual dimorphism in terms of body size is comparable, with *Saimiri* males also weighing around 19.7% (~0.62-1.2kg, $\bar{x}$=0.88kg) more than females (~0.60-0.88kg, $\bar{x}$=0.70kg).

In addition to differences in body size, *Cebus* spp./*Sapajus* spp. and *Saimiri* spp. also display other morphological variability, which relates to vertical stratification (see reviews in Sussman, 2000, 2003; Jack, 2011; Rylands & Mittermeier, 2013). For instance, although they are adapted for quadrupedal locomotion, they differ in their relative limb proportions. Unlike other Neotropical primates, *Cebus* spp./*Sapajus* spp. forelimbs and hind limbs are fairly equal in size, which has been suggested as an adaptation for their terrestrial locomotor patterns (e.g. Janson and Boinski 1992; Fleagle, 1999). Furthermore, their tails are semi-prehensile, which provide support (i.e. an anchor to a tree while foraging) and balance but cannot sustain the full weight of an adult (Fleagle, 1999; Sussman, 2000, 2003; Jack, 2011). Whereas *Saimiri* spp. have longer hind limbs, which is likely an adaptation for the more frequent leaping between trees and quadrupedal running that characterises their locomotion (e.g. Janson and Boinski 1992; Boinski, 1999; Fleagle, 1999), and though they are born with prehensile tails, the grasping ability is lost with age and is subsequently used to assist with balance (Boinski, 1989). In relation to the differences of their use of forest strata *Cebus* spp./*Sapajus* spp. are observed using the full spectrum of their vertical space, though they are rarely in emergent canopy or the shrub layer and only tend to visit the ground to forage, drink or travel (see Mittermeier & van Roosmalen, 1981). *Saimiri* spp. can also be found in all forest height levels, but generally they tend to be associated with densely foliated areas such as the forest understory (e.g. Mittermeier & van Roosmalen, 1981).

Cebus spp./*Sapajus* spp. and *Saimiri* spp. are considered to be omnivorous with some overlap in their overall diets (e.g. Mittermeier & van Roosmalen, 1981; Terborgh, 1983; Sussman, 2000, 2003; Boinski, 2002). Generally, when two closely related species have very similar ecological requirements (e.g. food, sleeping sites), they enter into interspecific competition, which can drive one of the two species to extinction (Schoener, 1988; Keddy, 1989). Therefore, in order for sympatric species to coexist without constant direct competition for resources they will need to adapt to different ecological niches (i.e. niche partitioning – see Charles-Dominique, 1977, Struhsaker, 1978; Fleagle et al., 1981; Mittermeier & van Roosmalen, 1981; Terborgh, 1983; Buchanan-Smith, 1999a). As discussed previously, in order for mixed-species groups to benefit from grouping the advantages need to outweigh the costs (see Section 1.2.). In order to gain from the double benefits of grouping there needs to be some ecological overlap for two or more species to form a mixed-species group (i.e. sympatric home ranges, same feeding trees), and shared predators (i.e. to benefit from grouping as a way of reducing individual predation) (Moynihan, 1976; Mittermeier & van Roosmalen, 1981). In the case of *Cebus* spp./*Sapajus* spp. and *Saimiri* spp. the latter tend to be more insectivorous in their diet, while the former are more frugivorous (which is also reflected in the differences in their dentition see Janson and Boinski 1992; Fleagle, 1999; Sussman, 2000, 2003; Jack, 2011), however both are able to become more specialised in response to changing environmental conditions (e.g. reduced fruit availability in the dry season). For example, *Saimiri* spp. are able to become completely insectivorous when fruit is unavailable, and *Cebus* spp./*Sapajus* spp. are able to live on bromeliads and/or become seed predators (see Kinzey, 1997a, 1997b; Sussman, 2000, 2003).

1.8 Group structure

All species of Cebidae live in multimale-multifemale groups, but their mating patterns, dispersal patterns and social structure vary (Boinski, 1999; Rylands, 2000; Boinski et al., 2003, 2005; Fragaszy et al., 2004; Jack, 2011; Rylands & Mittermeier, 2013). *Saimiri* spp. live in much larger group sizes than *Cebus* spp./*Sapajus* spp., with early studies reporting up to 300 monkeys (Baldwin & Baldwin, 1971, 1981 – see also Table 1.5), however further studies re-estimated the group sizes to range between 15-75 depending on the species (see Boinski, 1999; Boinski et al., 2003). This large discrepancy in number has been suggested to be due to a combination of the rapid locomotion of *Saimiri* spp. and their wide dispersion, in addition to reports of multiple groups coming together when food is scarce (Boinski, 1999; Sussman, 2000, 2003; Jack, 2011 – see also Table 1.5).

Prior to and during the annual mating season of *Saimiri* spp. the adult males undergo a dramatic physiological and morphological change, where they become 'fatted' gaining up to an extra 20% of their own body weight (DuMond & Hutchinson, 1967). This seasonal "fattening" of male body size is not however a result of accumulation of fat, as has been reported in rhesus macaques (*Macaca mulatta* – see Bercovitch, 1992; Jack, 2011), but from water retention-induced swelling in the upper torso, arms and shoulders (Mendoza, Lowe, Davidson & Levine, 1978; Boinski, 1987a, 1999; Jack, 2011; Stone, 2014). Male "fattening" is also not directly related to sperm production, as males are fertile year-round (Mendoza et al., 1978), but it does result in changes to hormonal levels within individual males, which has been linked to why there are more frequent and intense dominance interactions between males during the mating season (Baldwin, 1968). Ultimately the male that becomes the "fattest" is more desirable as a mating partner, and as such is more likely to have successful copulations with females in the group.

The social organisation of *Saimiri* spp. also differ between species, with the most extensively documented between *S. oerstedii, S. boliviensis* and *S. sciureus* (Boinski, 1999). For instance, *S. oerstedii* are described as being egalitarian as neither males nor females can be described as the dominant sex, and females emigrate from their natal group. Whereas in *S. boliviensis* females are dominant over males, and while there are stable linear dominance hierarchies in both sexes, males are generally peripheral and disperse from their natal group (sometimes joining bachelor groups – see Boinski, 1999). Finally, in *S. sciureus* both sexes form a single linear dominance hierarchy, all or most males are dominant over all females, and both sexes disperse from their natal group. Regardless of these inter-species differences, the social affiliations between *Saimiri* spp. appear to be the same across species and unlike other social primate species they are not based on grooming. Instead Rylands and Mittermeier (2013) stipulate that affiliations are maintained via proximity, tolerance at food sources, vocalisations (contact calls), and formation of alliances and coalitions to defend food patches.

Group sizes in *Cebus* spp./*Sapajus* spp. are smaller than *Saimiri* spp. and do not vary greatly between species, ranging between 10-27 individuals (see Rylands & Mittermeier, 2013 – see also Table 1.5) and unlike *Saimiri* spp. male dispersal from the natal group is the rule for all *Cebus* spp./*Sapajus* spp. (e.g. Strier, 1999; Fragaszy et al., 2004; Rylands & Mittermeier, 2013). Female *Cebus* spp./*Sapajus* spp. may also leave their natal groups, but this is observed less frequently (see Fragaszy et al., 2004). Due to females typically remaining in their natal group, *Cebus* spp./*Sapajus* spp. are generally characterised by female hierarchies, with affiliative bonds between females being stronger than those between males or between sexes, though they do appear to be relatively tolerant of conspecifics including non-kin (e.g. Cooper, Bernstein, Fragaszy & de Waal, 2001; Rylands & Mittermeier, 2013). While *Cebus* spp./*Sapajus* spp. do not have a clear linear hierarchy, males are typically dominant over females, with the exception of the alpha female who is often ranked directly below the alpha male and as such is dominant over all other males (Fragaszy et al., 2004; Rylands & Mittermeier, 2013). It is generally easy to distinguish the alpha male and female and the beta male, but after this it becomes less clear who holds the next position. However, the active avoidance of dominant individuals by subordinates can be a determinant of spatial positioning within the group. For instance, dominant individuals and infants/juveniles will most likely be found within the centre of the group, whereas subordinates will likely be on the periphery (Janson, 1990). As with most group-living animals, the position of *Cebus* spp./*Sapajus* spp. within their group can have important fitness consequences in relation to foraging success and vulnerability to predation (Janson, 1990; Fragaszy et al., 2004).

The social affiliations of *Cebus* spp./*Sapajus* spp. groups are mostly maintained by grooming, which has been shown to serve various social functions (Parr, Matheson, Bernstein & de Waal, 1997; Schino, Giuseppe & Visalberghi, 2009; Tiddi, Aureli, Schino & Voelkl, 2011; Tiddi, Aureli & Schino, 2012; Rylands & Mittermeier, 2013). Grooming rates in *Cebus* spp./*Sapajus* spp. have been shown to be related to coalitionary and dominance patterns, and influenced by reproductive cycles and kin relations (Parr et al., 1997; Schino et al., 2009; Tiddi et al., 2011, 2012; Rylands & Mittermeier, 2013). The alpha male is often the favoured recipient of grooming by both males and females in the group; males tend to groom less than females and hardly ever groom other males (Rylands & Mittermeier, 2013). Adult females will more often direct their grooming to other females (especially those with new infants) compared to other males (Tiddi, Aureli & Schino, 2010), and adjacently ranked individuals are also more likely to groom each other (Parr et al., 1997). Furthermore, the results of ‘rank-directional’ grooming in female *Cebus* spp./*Sapajus* spp. have shown that in wild groups of *S. apella nigritus* females groom up the hierarchy (e.g. Tiddi et al., 2012), while captive groups of *S. apella* groom down the hierarchy (e.g. Parr et al., 1997). Similarly, dominant female *C. olivaceus* tend to groom more, but are groomed less, and the reverse is found in *C. capucinus* and *C. imitator* (see Rylands & Mittermeier, 2013).

Within the context of mixed-species groups the larger *Cebus* spp./*Sapajus* spp. are considered dominant over *Saimiri*, because in aggressive encounters it is generally *Sapajus* who will chase away/displace the smaller *Saimiri* (e.g. Terborgh, 1983; Sussman, 2000, 2003). Group sizes vary between study sites (*Cebus* spp./*Sapajus* spp. *n*=2-16; *Saimiri n*=18-50), but generally there are more *Saimiri* than *Cebus* spp./*Sapajus* spp. (see Table 5.1). Preliminary studies indicated that *Cebus* spp./*Sapajus* spp. were taking the active role of seeking out *Saimiri* and maintaining mixed-species groups (e.g. Baldwin & Baldwin, 1971; Klein & Klein, 1973). However, Terborgh (1983) found that it was *Saimiri* who were seeking out *Cebus* spp./*Sapajus* spp., for example if *Saimiri* were leading group travel and *Cebus* spp./*Sapajus* spp. stopped or did not follow then *Saimiri* would circle back to rejoin them. Regardless of which species seeks out the presence of the other, this indicates a degree of social attraction, which has been considered a key feature of groups (see section 1.1). Both *Cebus* spp./*Sapajus* spp. and *Saimiri* appear to gain from the double benefits of grouping together (Pulliam et al., 1982 – see also Sections 1.3.1 and 1.6), though *Saimiri* probably benefit more by mixing with *Cebus* spp./*Sapajus* spp. relying more on their predator alarm calls (see Terborgh 1983, p.171):

“*…the response of* Saimiri *to* Cebus *alarms is generally much stronger than their response to their own calls.* Saimiri *often give alarm ‘peeps’ occasionally even in chorus, without provoking much reaction from the* Cebus*. The* Saimiri *may run or fling themselves out of the tree in panic, while the* Cebus *merely look up or continue their feeding.”*

1.9 Main aim of the study & thesis outline

There is a wealth of literature investigating the functions of mixed-species animal groups, with the majority agreeing on foraging advantages and reduced risk of predation as the two main drivers of grouping. However, as mentioned in the above summary there is a lack of consensus when it comes to defining or quantitatively characterising a group, especially when the duration, frequency and structure can vary so much between species. Therefore, rather than attempting to provide an all-encompassing definition of mixed-species groups, the main aim of this thesis is to provide, and test a framework that examines three of the four prerequisites for grouping (the prerequisite for a minimum of two individuals was disregarded, as it is given that there needs to be more than one individual in a group - see Section 1.1) and use different methodological approaches to quantify the groupness of mixed-species groups (see Figure 1.1). Capuchin (*Sapajus* spp.) and squirrel monkey (*Saimiri* spp.) mixed-species groups are one of the most well documented within the primate literature, and in addition to there being a number of different field sites where the monkeys can be observed in their natural habitats, there is also a mixed-exhibit housing two mixed-groups at the ‘Living Links to Human Evolution’ Research Centre in RZSS Edinburgh Zoo (hereafter Living Links). Together this make *Sapajus* spp. and *Saimiri* spp. ideal candidates for the purpose of this research.

The thesis is structured as follows. In Chapter 2 I discuss my six-month field study in Suriname, South America that I undertook in order to gain a better understanding of how my study species behave in the wild. I examined their use of forest strata, their vertical and horizontal group spread (i.e. their proximity in time and space – prerequisite 3) in conjunction with their behaviour in single- and mixed-species observations, (with a focus on foraging and vigilance (i.e. the double benefits of grouping). The frequency of mixed-species encounters was also documented but it was not possible to quantify group stability (prerequisite 1). In Chapter 3, I begin by describing the study site for the captive research that took place at Living Links, and the general methods used in the subsequent data Chapters 4-6 to examine and quantify ‘groupness’ in the two mixed-species groups of primates (see Figure 1.1).

Chapter 4 examines the monkeys’ use of three-dimensional space in their indoor and outdoor enclosures, using the modified spread of participation index (SPI – see Figure 1.1). In the wild *Sapajus* and *Saimiri* are often observed together in different levels of the canopy but still travelling in the same direction or foraging in the same trees. Studying their patterns of proximity in time and space use (an aspect of prerequisite 3) in captivity can help to determine whether they are behaving as a true mixed-species group, and if species are attracted or avoiding of each other. These data also provided an opportunity to see if captive monkeys were vertically stratified in a similar way to that observed in the wild.

In Chapter 5 I investigated synchrony in single- and mixed-species behaviour of *Sapajus* and *Saimiri* at the group-level allowing a thorough examination of the factors that might influence group behaviour, such as group size, age, sex, location and presence of the other species. The aim of this chapter was to examine the other aspect of prerequisite 3 (i.e. coordination in time and space), namely behavioural synchrony of both the single- and mixed-species groups at Living Links. It explores further how often the monkeys choose to be in shared spaces irrespective of available food (i.e. not aggregating around a resource or sharing space due to husbandry routines), and whether their behaviours are synchronised.

Chapter 6 examines the stability and socialness (prerequisites 1 and 2) of single- and mixed-species groups. Whilst Chapter 4 examines proximity in time and space in a more general sense (overlap in space use), this chapter is focussed on detailed proximities (i.e. within two body lengths - as a proxy measure for interactions) of individuals based on focal follows of each individual. Factors that might influence group social networks such as age, sex, kinship, rank and species were investigated. If the two species are behaving as true mixed-species groups, then it would be expected that there will be strong network ties (based on the frequency of being in proximity as a proxy for interactions) between species.

The final chapter (Chapter 7) provides a general discussion of the key empirical findings of this thesis and draws conclusions about what the evidence suggests in relation to the groupness of the monkeys at Living Links, and what this means for the study of mixed-species groups. In addition to this it explores how the findings relate more generally to welfare in captivity, and the methodological and theoretical implications. Finally, operational definitions are provided to distinguish between mixed-species groups, mixed-species associations, and aggregations.

2 LIVING WILD LINKS

2.1 Abstract

There are a range of benefits to using a combined captive-field approach to research. Captive and field studies both provide valuable and complementary information that lead to a better understanding of a species' behavioural ecology. For instance, captive environments such as zoos provide a controlled environment that facilitates longitudinal studies of behaviour and reproduction, and provides opportunities to collect data on life history, which may be more difficult in the wild (i.e. animals missing due to predation, illness). Field studies can provide some context relating to the adaptive nature of behaviours that are studied in captivity. In this Chapter I evaluate the usefulness of conducting field work alongside captive research and describe an exploratory study of the behavioural ecology of tufted capuchin (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) at two field sites (the Raleighvallen Nature Reserve and Peperpot Nature Reserve) in Suriname, South America. There were fewer mixed-species sightings than single-species at both sites. Linear models (LMs) and linear mixed models (LMMs) found that the proportion of vigilance observed in *Saimiri* was higher at both field sites compared to *Sapajus*, but that overall vigilance was lower in mixed-species groups compared to single-species groups. While the proportion foraging was higher for *Sapajus* at the two sites compared to *Saimiri*, overall foraging was lower in mixed-species groups compared to single-species groups. These findings provide support for antipredatory benefits of grouping but not foraging advantages. The discussion focusses on how the combined captive-field approach can be used to examine environmental factors that may affect the groupness of *Sapajus-Saimiri* mixed-species groups.

2.2 Introduction

2.2.1 *A combined field-captive approach to studying mixed-species groups*

An animal's ability to move and interact with both their environment and with other animals (conspecifics and heterospecifics) enables them to adapt to the environments in which they live. These adaptations can take many different forms (e.g. predator avoidance, attracting a mate, dominance challenges, and rearing offspring) and each species, and even individuals of the same species, will have different requirements. Understanding the ways in which animals are adapted to their respective environments will enable us to gain crucial insights for maintaining viable populations in captivity. It is generally accepted that captive animals live in environments that are substantially different from that which they evolved in the wild, such as differences in; climate and seasonality, habitat (e.g. forest, savannah, ocean), range or territory size, diet (including the method of procuring food), risk of predation, and the formation and maintenance of groups (Hediger, 1950; Kleiman, 1989; Buchanan-Smith & Hardie, 1997; Kerridge, 2005; Zimbler-DeLorenzo & Stone, 2011).

Behaviour, as with morphology and physiology, evolves in complex environments in order to increase the likelihood of an individual's survival and ultimately their reproductive and inclusive fitness. Therefore, captive animals will likely adjust their behaviour(s) in order to adapt to their given environments, which could potentially lead to genetic and phenotypic divergence between captive and wild populations (Darwin, 1964; Price, 1984, 1998; Lickliter & Ness, 1990; McPhee, 2003a, 2003b, 2004; McPhee & Carlstead, 2010). According to McPhee and Carlstead (2010) these responses to the captive environment can occur on three levels: (1) an individual can change their behaviour in order to meet an immediate and specific need, such as conforming to husbandry and feeding schedules or to conspecific groupings; (2) animals that are born in a captive environment (which is often more restrictive than the wild) may develop differently, altering how they learn and respond to events; (3) within a captive population, certain behaviours will lead to increased survival rates on the individuals who express them (e.g. greater tolerance to loud/unexpected noises or close proximity to humans). These behaviours are likely to be passed on across generations through social learning (see Whiten & Ham, 1992; Custance, Whiten & Fredman, 2002), resulting in a distribution of traits within the captive population that are distinctly different from those observed in wild populations. At the extreme there may also be genetic modifications if species have been held in captivity for many generations. Those individuals that cannot cope with captivity (e.g. very nervous individuals) do not breed, whilst those best suited go on to produce offspring, affecting the genetic diversity. Captive breeding programs in zoological parks should therefore be equally concerned with conserving behaviours as well as genes (Kerridge, 2005), especially as all three levels of change may compromise both *ex situ* and *in situ* conservation efforts, as well as the ecological validity of captive based research (e.g. studies on sociality and cognition). Thus, maintaining natural species-specific behaviours in captive-bred populations should be a priority for zoological parks, if their goal is to reintroduce animals into their natural habitats (Kleiman et al., 1986; Box, 1991; Kerridge, 2005; Keulartz, 2015; Howell & Cheyne, 2019).

However, for the most part, many animals within zoological parks are unlikely to be reintroduced to the wild, which begs the question of whether promoting and maintaining natural species-specific behaviours should really be an important consideration. In short, yes it should. For many zoos there has been a shift in focus of their mission statement(s), from the "Noah's Ark" paradigm (i.e. maintaining viable populations in captivity that can be reintroduced to the wild), to supporting conservation projects *in situ* (e.g. World Conservation Union, 1987; IUDZG, 1993; Hutchins & Conway, 1995; Koontz, 1997; Keulartz, 2015). In addition to this, zoos have also adopted education, science, and recreation as part of their mission statement(s), and a large part of achieving this is to ensure the proper care and welfare of their animals (Hosey, 2005; Rees, 2011; Bowler, Buchanan-Smith & Whiten, 2012; Mellor, 2016; Howell & Cheyne, 2019). The presence of species-specific behaviours in captive animals is a potential indicator that (1) its needs are being met (2) the captive environment is suitable, and (3) that overall it has good health, good well-being, and as a result can be described as having 'good' welfare (Gold, 1997; Mellor, 2016).

Modifying the captive environment to mimic key features of their wild habitat is one way to encourage more species-typical behaviours, and may also decrease aggression and abnormal or stereotypical behaviours (Baker, 1997; Gold, 1997; Jendry, 1997; Hosey, 2005; Leonardi, Buchanan-Smith, Dufour, MacDonald & Whiten, 2010; see also Chapter 4). Many zoos have been able to achieve this by building more naturalistic enclosures (e.g. vertical structures for arboreal animals to encourage climbing, clinging and/or leaping, vertical stratification), providing enrichment that is either environmental (devices that encourage active foraging, or providing materials for nest building) or social (mixed-species exhibits), and (where appropriate) allowing animals to have the choice of accessing both indoor and outdoor enclosures (Gold, 1997; Jendry, 1997; Buchanan-Smith, 2012; Mellor, 2016 - see also Chapter 4). However, in order to do this most effectively it is important to first understand how the animals under their care behave and interact in their wild environment(s), which is why field research is so important.

The majority of animals live in complex ecosystems, coexisting with members of their own species as well as numerous other fauna and flora. Using a combined field-captive approach to animal behaviour research can provide valuable and complementary information, which will help us to better understand the ultimate and proximate causes of an animal's behavioural ecology. This approach to research is not a new concept; Tinbergen (1963) noted its importance for better understanding an animal's behaviour. Several modern zoos now have exhibits that are affiliated with a field site (see Table 2.1). Field research enables scientists to observe animals behaving in their natural environment, allowing for a more inductive (and bottom-up) approach to data collection (Tinbergen, 1963; Krebs & Davies, 1993; Zimbler-DeLorenzo & Stone, 2011). Captive studies on the other hand, allow us to test hypotheses derived from field research under controlled conditions. The captive environment can also help us to better understand aspects of species-specific behaviours that are rare, or difficult to observe in the wild, due to observations taking place in a comparatively much smaller and controlled environment (Baldwin, 1985; Carlstead, 1996; Buchanan-Smith & Hardie, 1997). A further advantage of conducting research in captive environments (e.g. zoological parks or research colonies) is that longitudinal studies of behaviour and reproduction are easier to conduct in captivity than in the wild because physiological and life history data are generally known for all individuals (Fairbanks & McGuire, 1984; Kleiman, 1992; Hardy, 1996; Fedigan, Carnegie & Jack, 2008; Jack and Fedigan, 2004a, 2004b; Strier & Mendes, 2009; Buchanan-Smith, Griciute, Daoudi, Leonardi, & Whiten, 2013).

Tufted capuchins (*Sapajus* spp.) and squirrel monkeys (*Saimiri* spp.) have been frequently observed together in the wild and have been described as forming mixed-species groups (e.g. Klein & Klein, 1973; Fleagle, Mittermeier & Skopec, 1981; Terborgh, 1983; Podolsky, 1990), but as discussed in Chapter 1 (see Sections 1.1 and 1.4) there are inconsistencies in the literature as to how the 'groupness' of *Cebus* spp./*Sapajus* spp. – *Saimiri* spp mixed-species groups is defined and measured. Generally, studies have used the following criteria to define mixed-species sightings, whereby the different monkey species are within <20m or <50m and intermingled (e.g. Terborgh, 1983; Podolsky, 1990). Studies investigating habitat use and diet/resource use of *Sapajus* spp. and *Saimiri* spp. (e.g. Fleagle et al., 1981; Mittermeier & van Roosmalen,1981; Terborgh, 1983; Podolsky, 1990), note that while both species were observed in all sections of the forest canopy (e.g. understory, lower, middle, upper and emergent) *Sapajus* spp. were commonly found in middle and lower levels, while *Saimiri* spp. were found predominantly in the understory. The differences in space use can be directly related to the differences in their body size, locomotor behaviour and diets (see Section 1.7), but could also be influenced by the presence of the other species (e.g. foraging advantages for *Saimiri* in the presence of *Sapajus* – see Terborgh, 1983 and Section 1.6). It is therefore important to consider comparisons of individuals in single- and mixed-species groups, in order to allow us to understand better the impact that one has on the other (e.g. Terborgh, 1983; Buchanan-Smith & Hardie, 1997). Therefore, if we want to learn more about both single- and mixed-species groups in terms of their natural behaviours and the environments in which they live (and how they interact in them), then it is important to first observe them in the wild. This will then help with research conducted in captivity, as researchers will have a better inclination of the type(s) of behaviours to look out for, and whether or not enclosure space(s) are sufficient (i.e. provide key elements of the natural environment) and encourage naturalistic species-specific behaviour(s).

Table 2.1 *Examples of zoological parks in the UK and USA that have connections with field sites/research projects.*

<table>
<tr><th>Zoological Park</th><th>Exhibit/Species</th><th>Field project</th></tr>
<tr><td>Royal Zoological Society Scotland, Edinburgh Zoo, UK</td><td>Budongo Trail, Chimpanzees (<i>Pan troglodytes</i>)</td><td>Budongo Forest, Uganda, Africa</td></tr>
<tr><td colspan="3">see https://www.edinburghzoo.org.uk/animals-and-attractions/main-attractions/budongo-trail/</td></tr>
<tr><td>Chester Zoo, UK</td><td>Asian elephants (<i>Elephas maximus</i>)</td><td>Management and ecology of Malaysian elephants (MEME), South East Asia</td></tr>
<tr><td colspan="3">See: https://www.chesterzoo.org/what-we-do/our-projects/management-and-ecology-of-malaysian-elephants-meme/</td></tr>
<tr><td>Chester Zoo, UK</td><td>Spider monkey (<i>Ateles fusciceps ruiventris</i>)</td><td>Spider Monkey Project, Latin America</td></tr>
<tr><td colspan="3">See: https://www.chesterzoo.org/what-we-do/our-projects/spider-monkey-project/</td></tr>
<tr><td>Zoological Society London, London Zoo</td><td>Slender loris (<i>Loris</i> sp.)</td><td>Red Slender Loris Conservation Programme (RSLCP)</td></tr>
<tr><td colspan="3">See: https://www.zsl.org/conservation/regions/asia/saving-slender-lorises-in-sri-lanka</td></tr>
</table>

Table 2.1 *continued.*

San Diego Zoo, USA	Giant otter (*Pteronura brasiliensis*)	Giant otter conservation program, Cocha Cashu Biological Station, Peru
See: https://institute.sandiegozoo.org/species/giant-otter		
Lincoln Park Zoo, USA	Chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla* sp.)	Goulougo Triangle Ape Project, Democratic Republic of the Congo, Africa
See: https://www.lpzoo.org/conservation-science/projects/goualougo-triangle-ape-project		

This chapter is about my field research in Suriname, South America, which I conducted in order to gain a better understanding of how my study species: Guianan tufted capuchins (*Sapajus apella*) and Guianan squirrel monkeys (*Saimiri sciureus*) behave in the wild. The underlying aim of this research was to collect general demographic data on the behaviour and habitat use of *Sapajus* and *Saimiri* at two different study sites in Suriname: (1) the Raleighvallen Nature Reserve (primary forest), and (2) Peperpot Nature Reserve (secondary forest). The two sites were selected in order to gain a better understanding of variation in wild troops in relation to their environments, and their behavioural flexibility. I was particularly interested in data on habitat use, vertical stratification and intergroup encounters/interactions, as potential factors for measuring 'groupness' of mixed-species groups in captivity (see Chapters 4-6). I also wanted to collect basic demographic data on the other 6 sympatric primate species (*Saguinus midas, Cebus castaneus, Pithecia pithecia, Chiropotes sagulatus, Alouatta macconnelli* and *Ateles paniscus*), in order to gauge whether the *Sapajus-Saimiri* association was impacted by the presence of other species, or whether other mixed-species groupings were observed.

Primary aims of the field study were:

1. To collect data on the main group parameters such as group size and group spread (vertical and horizontal - proximity in space and time) of *Saimiri* and *Sapajus*.
2. To collect data on activity patterns (single- and mixed-species observations), vertical stratification and habitat preference of *Saimiri* and *Sapajus*. Following Podolsky (1990) mixed-species sightings included when *Sapajus* and *Saimiri* were observed ≤20m.
3. To collect data on rates and durations (stability) of mixed-species groups of *Saimiri* and *Sapajus*.

4. To evaluate the structure and composition (e.g. vegetation types and canopy cover) of the study site.
5. To collect basic demographic data on the other 6 sympatric primate species.

Secondary aims were to scope the potential for developing the Raleighvallen Nature Reserve into a long-termed linked field site to the Living Links to Human Evolution Research Centre, RZSS, Edinburgh Zoo and to improve on my knowledge and experience of field techniques.

2.3 Methods

The field study was conducted in Suriname, South America. The main site was in the Raleighvallen Nature Reserve approximately 216km south of the capital Paramaribo. Further observations were made at a subsidiary site called the Peperpot Nature Park, which was in the district of Commewijne.

2.3.1 Suriname & the Guiana Shield

The Republic of Suriname (hereafter Suriname) is part of the Guiana Shield (one of three cratons of the South American Plate), which encompasses much of the north-eastern corner of South America (Figure 2.1). Bordered by the Orinoco, Rio Negro and Amazon rivers it includes all or parts of the following countries: Venezuela, western Colombia, the Co-operative Republic of Guyana (hereafter Guyana), Suriname, French Guiana and northern Brazil (Raghoenandan, 2000). It is a region that has become globally known for its intact and relatively unexploited tropical rainforest within a geologically ancient (Precambrian) landscape (Hammond, 2005).

Suriname lies on the north-eastern Atlantic coast of South America, covering an area of approximately 165,000km^2. It is bordered by French Guiana to the east, Brazil to the south and Guyana to the west (Figure 2.1). Situated just above the equator (between 2° and 5° northerly latitude), Suriname can be divided into three topographical regions: the low-lying coastal plains; the inland elevated plateau, wide forest-covered river valleys and savannahs; and the Guiana Highlands, maximum altitude reaching 1,280m (Brawer, 1991). Suriname is also divided by a number of major river systems (and their tributaries), with most of them flowing from south (Guiana Highlands) to north (the coast). The rivers from east to west of the country are: the Corantijn (bordering Guyana); Nickerie; Coppename; Saramacca;

Suriname; Commewijne and the Marowijne (bordering French Guiana). The northern portions of the rivers and those that run parallel to the coast are wide and slow, whereas the upper reaches within the interior are crisscrossed by numerous rapids and waterfalls (Duplaix, 1980).

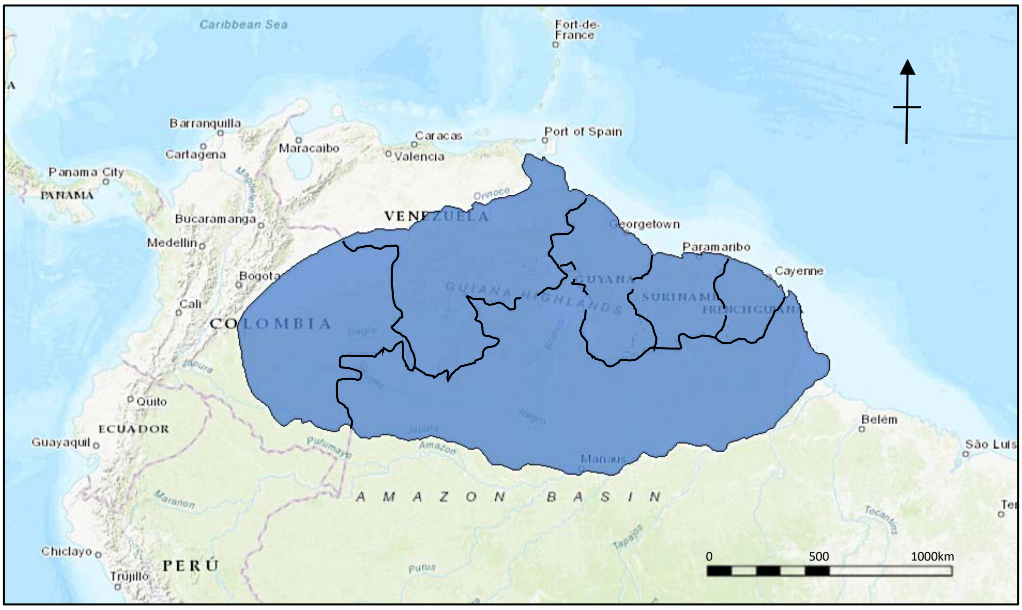


Figure 2.1 Topographic representation of the Guiana Shield within the north-eastern corner of South America (created in ArcGIS).

2.3.2 Climate

According to the Köppen-Geiger climate classification, Suriname has a fully humid, equatorial rainforest climate, with one or more months of ≥60mm of rain and high annual precipitation (Kottek, Grieser, Beck, Rudolf & Rubel, 2006). The mean temperature (see Figure 2.2) ranges between 23-36°C throughout the year, with 80-90% humidity (which can make temperatures feel up to 6°C warmer) and mean annual rainfall (see Figure 2.2) between 2000-2500mm (Baal, Mittermeier & van Roosmalen, 1988; Nurmohamed, Naipal & Becker, 2007). There are usually two wet seasons: April-August and November-February, and two dry seasons: August-November and February-April. However, the onset and duration of these seasons can vary from year to year due to climatic factors, such as the Pacific El Niño-Southern Oscillation (ENSO), the Atlantic zonal equatorial mode (tropical Atlantic Niño) and the tropical Atlantic meridional gradient (TAMG) (Nurmohamed et al., 2007).

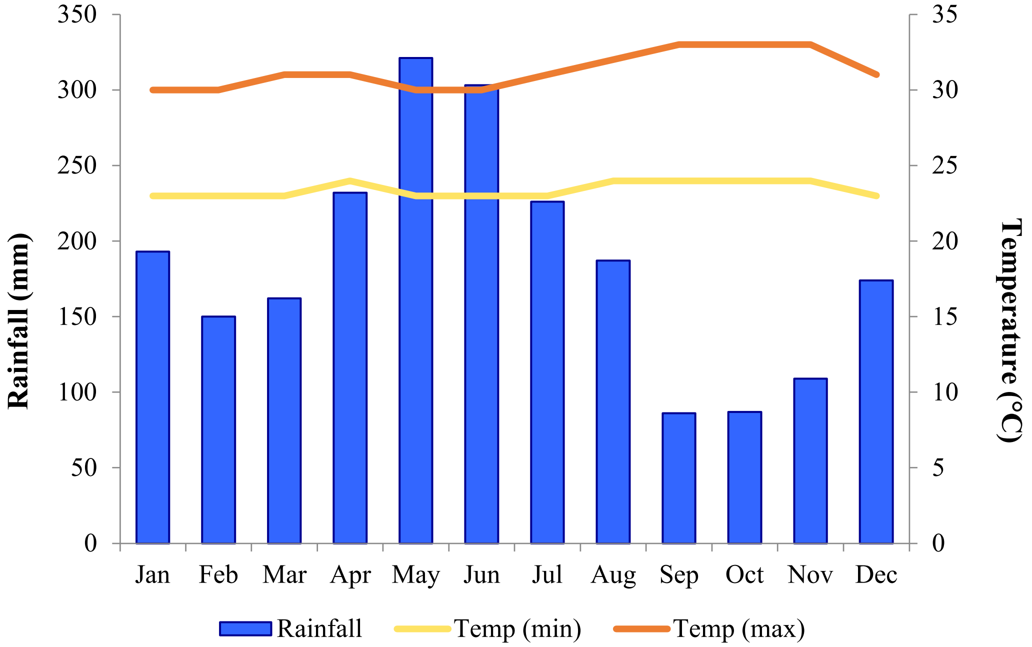


Figure 2.2 Mean monthly rainfall (mm) and mean monthly minimum and maximum temperature (°C) in Paramaribo, Suriname for 2017 (Data taken from World Weather & Climate Information).

2.3.3 Central Suriname Nature Reserve

Suriname is fortunate to have much of its interior forest still intact (approximately 15.3 million hectares) covering 94% of the country's surface area and ~91% of this is primary forest (FAO, 2015), with more than 1.6 million ha (approximately 10% of the country and 80% of all protected areas in Suriname) making up the Central Suriname Nature Reserve (CSNR) (Figure 2.3). It encompasses three pre-existing reserves: the Raleighvallen Nature Reserve (78,000 ha), the Tafelberg Nature Reserve (140,000 ha) and the Eilerts de Haan Gebergte Nature Reserve (220,000 ha) and is one of the largest protected tropical forest areas within South America (SCF, 2012). The CSNR was established in 1998 with the Government of Suriname firstly imposing only a temporary prohibition on large-scale logging operations in critical ecosystems and later creating a fully protected area (SCF, 2012). Through the combined efforts of local, national, and international stakeholders, the CSNR became recognised as a significantly biodiverse region, and in 2000 gained UNESCO World Heritage status.

Figure 2.3 Topographic representation of the Central Suriname Nature Reserve (CSNR), Suriname, South America (created in ArcGIS).

The montane and lowland forests of the CSNR contain a high diversity of plant life with almost 5,000 vascular plant species collected to date, many of which are endemic (Baal et al., 1988; Berry, Huber & Holst, 1995; UNESCO, 2017a). There are also areas of swamp forest, savannah and xerophytic vegetation on the granite outcrops and inselbergs (Berry et al., 1995; Huber, 2005). The reserve's vegetation consists mostly of moist mesophytic 'primary' forest, with a large variety of tree species, including some of the tallest in South America such as the kapok (*Ceiba Pentandra*), greenheart (*Chlorocardium rodiei*) and Indian pipe (*Monotropa uniflora*) trees, to name a few (UNESCO, 2017b). The uppermost canopy averages at approximately 30 meters (but can reach 40-50 meters), with palms (e.g. *Attalea maripa* and *Astrocaryum sciophilum*) mostly dominant in the undergrowth, and ferns and moss-ferns sparsely populating the forest floor (UNESCO, 2017b).

The area is mostly unaffected by anthropogenic activities and as such remains in relatively pristine condition (UNESCO, 2017a), which makes it an extremely valuable baseline for biological and ecological research. The Nature Conservation Division (NB) forms part of the Suriname Forest Service (LBB), which is a governmental agency responsible for the management of all nature reserves in Suriname, and for handling all matters relating to nature conservation, including policy making and law enforcement (SCF, 2012; UNESCO, 2017a).

However, due to the sheer size of the CSNR and a lack of adequate resources, it has become increasingly difficult to uphold law enforcement of forestry, wildlife and nature conservation. Eco-tourism provides some potential for localized interventions, but this is unlikely to significantly contribute to covering management costs. Arguably the most pressing long-term challenges will be down to the rich mineral (e.g. bauxite, gold and diamonds) and timber resources in and around the CSNR, several exploratory mining and logging concessions have already been granted to the North, East and West (Baal et al., 1988; SCF, 2012; UNESCO, 2017a).

2.3.4 Fauna

Although the diversity of Suriname's fauna is not as high as that of other countries in South America (e.g. Brazil or Peru), it can still be described as rich in vertebrate wildlife, with 1,215 known species (birds: 674, mammals: 200, reptiles: 152, amphibians: 99 and fish: 90), approximately 3% of which are endemic (Baal et al., 1988; SCF, 2012; UNESCO, 2017a, 2017b). There are a number of charismatic species listed by the IUCN Red List of Threatened Species (hereafter IUCN Red List) from Least Concern (Guianan cock-of-the-rock (*Rupicola rupicola*), scarlet macaw (*Ara macao*), blue-and-yellow macaw (*Ara ararauna*), two-toed sloth (*Choloepus didactylus*), three-toed sloth *Bradypus tridactylus*), southern tamandua (*Tamandua tetradactyla*) and porcupines (*Coendou prehensilis* & *C. melanurus*)) and Near Threatened (harpy eagle (*Harpia harpyja*), Guiana river dolphin (*Sotalia guianensis*) A2d+3d+4d, and jaguar (*Panthera onca*)) to Vulnerable (giant armadillo (*Priodontes maximus*) A2cd, giant ant eater (*Myrmecophaga tridactyla*) A2c, and lowland tapir (*Tapirus terrestris*) A2cde+3cde), and Endangered (giant river otter (*Pteronura brasiliensis*) A3ce) (IUCN, 2020).

The region is also home to eight sympatric species of primate (see Table 2.2) (Baal et al., 1988). *Ateles paniscus* is listed as Vulnerable on the IUCN Red List (Mittermeier, Rylands & Boubli, 2019; IUCN, 2020), with the remainder listed as Least Concern (Boubli, Rylands, de la Torre & Stevenson, 2008; Boubli et al., 2018a; Boubli, Mittermeier, Urbani & de Azevedo, 2018b; Marsh et al., 2018; Mittermeier & Rylands, 2018; Mittermeier, Rylands & Boubli, 2018; Cortes-Ortíz et al., 2020 IUCN, 2020).

Table 2.2 *The conservation status of Suriname primates as listed on the current IUCN Red List of Endangered Species version 2020-2 (LC = Least Concern, VU = Vulnerable). All weights are based on adult animals; ♂= male ♀ = female (Ford & Davis, 1992; Fleagle, 1999; Campbell et al., 2011).* *C. sagulatus *resurrected - takes up most of former range of* C. chiropotes *(A. Rylands, personal communication, December 28, 2015).*

Family	**Latin name**	**Common & *Sranan (local)* name**	**$\bar{x}$ Size (g) ♂ / ♀**	**$\bar{x}$ Group size**	**Home range (ha)**	**Conservation status**
Callitrichidae	*Saguinus midas*	Golden-handed tamarin *(Saguwenke)*	515 / 575	6	31-42	LC — Stable
Cebidae	*Saimiri sciureus*	Guianan squirrel monkey *(Monkimonki)*	779 / 668	15-50	110-300	LC ↓Decreasing
	Sapajus apella	Guianan brown tufted capuchin *(Keskesi)*	3650 / 2520	18	200	LC ↓Decreasing
	Cebus olivaceus	Guianan weeper capuchin *(Bergi Keskesi)*	2974 / 2345	21	200	LC — Unknown
Pitheciidae	*Pithecia pithecia*	White-faced saki *(Wanaku)*	1732 / 1515	3.2	10.3	LC ↓Decreasing
	*Chiropotes sagulatus**	Guianan bearded saki *(Bisa)*	2900 / 2580	8-30	200	LC — Stable
Atelidae	*Alouatta macconnelli*	Guianan red howler monkey *(Babun)*	6690 / 5210	6-8	4-20	LC — Unknown
	Ateles paniscus	Red-faced black spider monkey *(Kwata)*	9110 / 8440	18	200	VU(A4cd) ↓Decreasing

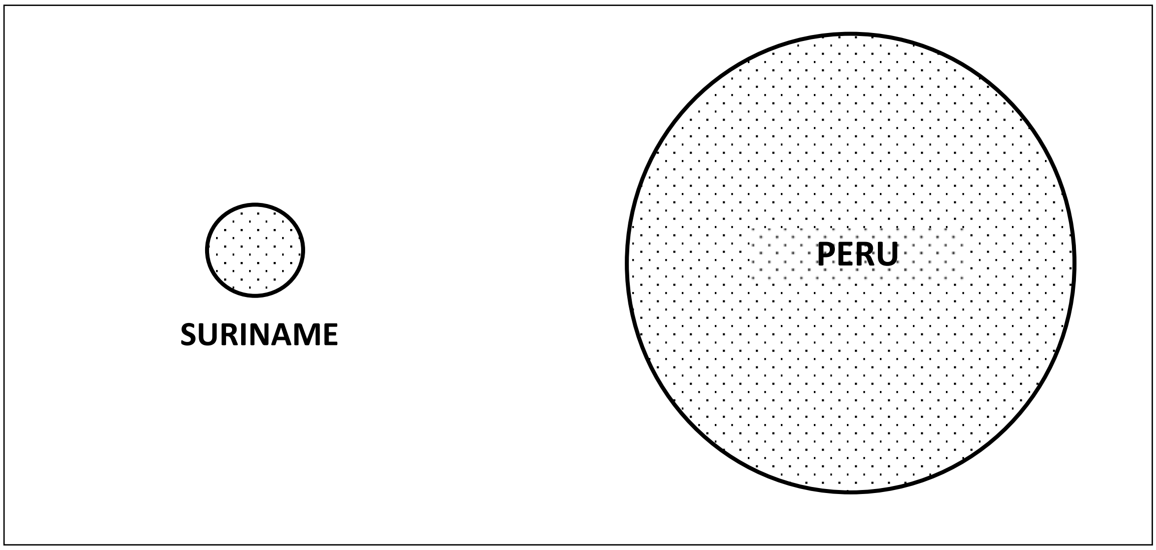


Figure 2.4 *Graphic representation of the density of forest fruits encountered in Suriname, and Peru. The diameter of the circle indicates the relative size of the fruit patch (breadth of tree or shrub crown bearing ripe fruit) and the density of dots within the circles represent the relative density of fruits within that patch. Therefore, fruit patches in Suriname are comparatively small but at the same time dense, whereas in Peru, fruit patches are both large and high in density (taken and adapted from Boinski, 1999).*

The amount of edible fruit-producing trees in Suriname, while dense is comparatively small when compared with that of Peru (see Figure 2.4), yet due to niche partitioning there is relatively low competition between primate species for resources. Though diets vary between species, there are some overlaps (see Figure 2.5) with all monkeys encompassing at least soft pulp fruits, which highlights their importance as seed dispersers via either endozoochory, when the seeds are swallowed intact without mastication, and still able to germinate after excretion, and/or exozoochory when seeds are carried and dropped at another location) (Mittermeier & van Roosmalen, 1981; Chapman, 1989, 1995; Garber & Lambert, 1998; Lambert & Garber, 1998; Norconk, Grafton & Conklin-Brittain, 1998; Chapman & Russo, 2011). Contrasting with seed dispersal is seed predation, where the seeds are no longer able to germinate due to being chewed into a mealy pulp; *Saguinus, Cebus*, *Sapajus, Chiropotes* and *Pithecia* are known seed predators (see Mittermeier & van Roosmalen, 1981). Additionally, primates are a source of food for terrestrial predators such as felids: jaguars (*Panthera onca*), pumas (*Puma concolor*), ocelots (*Leopardus pardalis*) and margays (*Leopardus wiedii*) and snakes: boa constrictors (*Boa c. constrictor*), rainbow boas (*Epicrates cenchria*) and venomous snakes (e.g. Boinski, 1988b; Tello, Huck & Heymann, 2002). Aerial predators include harpy eagles (*Harpia harpyja*) and crested eagles

(*Morphnus guianensis*) (Frechette, Sieving & Boinski, 2014). Therefore, it can be inferred that the monkeys and the ecosystem in which they live are intricately linked.

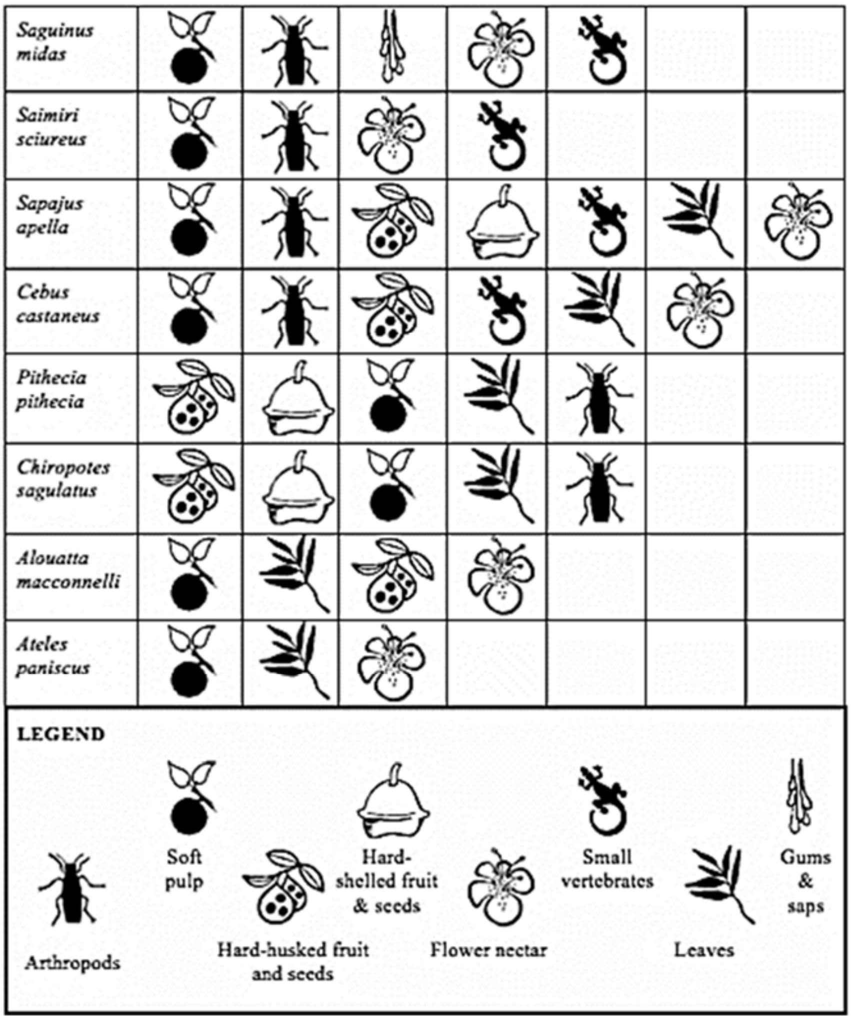


Figure 2.5 Type of foods eaten by the 8 Suriname primates listed from left to right in order of importance, taken and adapted from Boinski (2002).

2.4 Study sites

2.4.1 Raleighvallen Nature Reserve

The primary study was conducted at the Raleighvallen Nature Reserve (04° 42.955’N, 056° 12.660’W), within the CSNR. The terrain was predominantly tropical primary forest, which has been previously classified into five distinct habitat types: (1) Liana forest, which is comprised predominantly of lianas and vines; (2) High rain forest, encompasses taller trees (emergent trees reaching 40-45m), palms are more common (e.g. *Astrocaryum sciophilum*) and there are fewer lianas. High forest is probably the most important habitat for primate species as it includes more edible fruit-producing species than any other formation; (3) Low rain forest, trees do not usually exceed 20m in height, richer in lianas and fewer palms; (4) mountain savannah forest, occurs on bauxite hills and low mountains (inselbergs), consisting of xeromorphic species such as bromeliads (*Bromelia alta*), cacti (*Cereus hexagonus*) and some taller trees (usually intermediary to high forest); (5) Swamp forest, which has a similar structure to the high forest, with seasonal standing water (in the rainy season) and plants that are adapted to seasonal flooding (for more detailed descriptions see Mittermeier & van Roosmalen, 1981). There are also a number of continuous, dense and homogenous patches of bamboo (*Guadua latifolia*), which are an important resource for *Sapajus* (Frechette et al., 2014). The fruiting season begins in January, lasting through to April, with the onset of the wet season beginning in May through to August (Mittermeier & van Roosmalen, 1981; Frechette et al., 2014). Elevations of the study area ranged between 11-106m.a.s.l. Access to the site is either by car/bus from Paramaribo to Witagron and then a boat (approx. 8 hours) or by plane from Paramaribo (approx. 2-3 hours).

2.4.2 Peperpot Nature Park

Data collection at the Raleighvallen Nature Reserve ended prematurely in March 2017, due to unforeseen circumstances (logistical errors in equipment and injury). However, this provided me with the opportunity to collect additional, secondary data on a troop of *Sapajus* and *Saimiri* in order to determine the variation in behaviours in the wild. The Peperpot Nature Park (820 ha), Commewijne district (5.7750° N, 55.1106° W) was previously a plantation, cultivating sugar cane, coffee and cocoa, and is now an area of secondary forest. Coffee (*Coffea arabica*) and cacao (*Theobroma cacao*) trees are still present, along with indigenous fruiting trees such as mope (*Spondias mombin*) and boesipapaja (*Cecropia obtuse*) and large bamboo patches (*Guadua angustifolia*). In 2009 in a joint conservation effort by WWF Guianas and the Surinamese Cultural Society N.V. (Mariënburg) the Peperpot Nature Park established (Peperpot Nature Park, 2017; WWF, 2017). There was only one accessible trail (Mopentibo Nature Trail) approximately 3.2km in length (Figure 2.6), with irrigation ditches on either side.

Figure 2.6 Photos of the Mopentibo Nature Trail and vegetation at the Peperpot Nature Park (photos taken by S.D).

2.4.3 Trails - Raleighvallen Nature Reserve

Trails were established at the study site in early December 2016, prior to the start of the study. Placement of the trails would utilise the existing Voltzberg trail, starting ~100m from the river and extend for approximately 5km from this point. Originally six line transects were to be cut perpendicular to the Voltzberg trail (approximately 2km), with approximately 1km between starting (Buckland et al., 2001; Sutherland, 2006). These distances were chosen to enable surveying within four of the five different vegetation types at the site: high forest, liana forest, savannah forest and *Pina* swamp forest. However, due to physical obstructions (e.g. large bamboo patches, dense lianas, large stones) traditional line transects and grids could not be applied, as an alternative 'path of least resistance' transects were used (Hall et al. 1997; White & Edwards, 2000; Blake, 2002; Blake & Inkamba-Nkulu, 2004; Weinbaum, Nzooh, Usongo & Laituri, 2007). Six zones (A1, B1, C1, A2, B2 and C2) were mapped out (see Figure 2.7). Each zone had a trail running through it 2-3km in length, which would loop back on to the Voltzberg trail. Biodegradable tape was used for placing markers on trees (every 5 paces) along each trail.

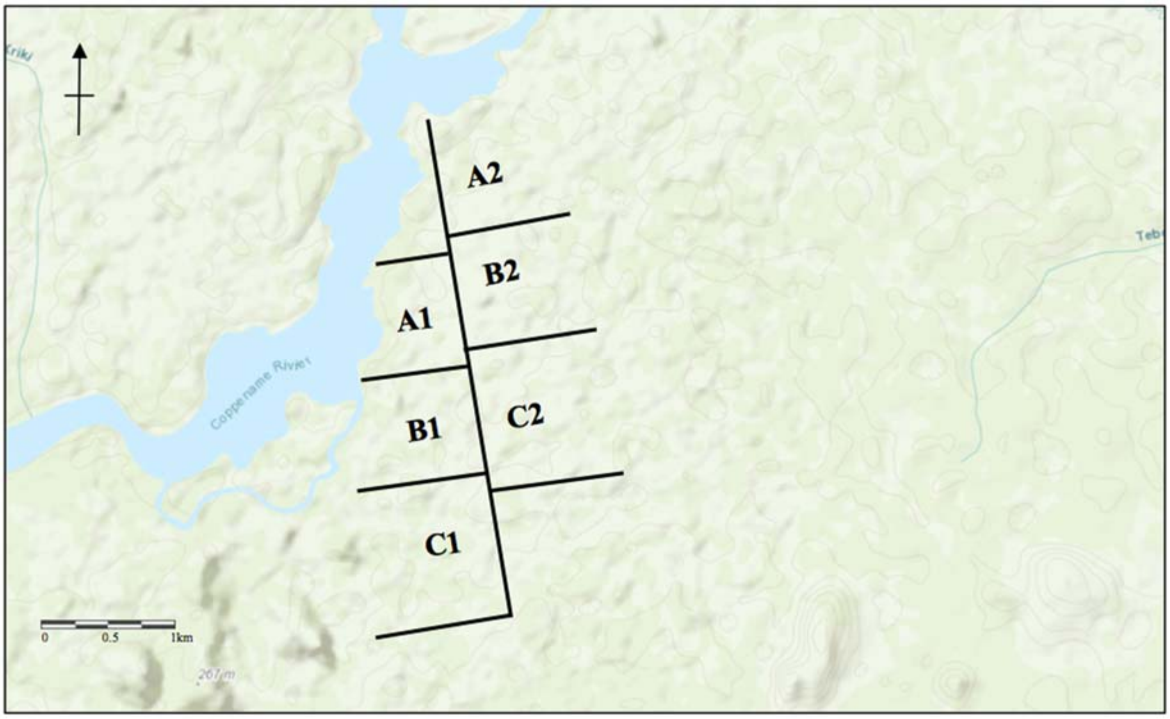


Figure 2.7 Study site zones at the Raleighvallen Nature Reserve, with the central line representing the pre-existing Voltzberg trail (not to scale). All grid lines are based on approximations (created using ArcGIS). **A1** (predominantly pina swamp forest and close to the river), **B1** (predominantly palm forest), **C1** (predominantly palm forest with some liana, low and high forest), **A2** (palm forest with some liana and low forest), **B2** (predominantly palm forest, with some liana, low and high forest), **C2** (predominantly palm forest, with some liana, low and high forest), **Voltzberg** perpendicular trail (encompasses elements of each of the habitat classifications) see Figure 2.15 for more details on habitat for each trail.

2.4.3.1 Habitat classification & vegetation

Habitat categories were subjectively assigned to best represent the immediate environment within each zone (following Mittermeier & van Roosmalen, 1981). Most of the categories were based on vegetation structure and in some instances a distinctive flora. The following six categories were used:

(1) Liana forest: tall trees do occur here (≤30m) but they are widely separated from one another and no true canopy exists. The spaces between trees are filled with dense tangles of lianas and vines (see Figure 2.8), which rarely exceed 10-15m and are classed as understory in vertical stratification observations. This forest type provides microhabitats for various insects and arthropods, which makes it a good place to forage for small insectivorous primates (see Figure 2.5).

Figure 2.8 Examples of lianas in the Raleighvallen Nature Reserve (photos by S.D).

(2) *Pina* swamp forest (Figure 2.9): the soil stays moist throughout the seasons (either under water or at least damp during the peak of the dry season). Lianas and epiphytes are not common, but stilt roots on trees are. *Pina* palms (*Euterpe oleracea*) dominate the area and grow in small clusters (generally no higher than 15-20m). Also includes some maripa palms (*Attaleae maripa*) and lebi-loabi (*Eschweilera corrugata*).

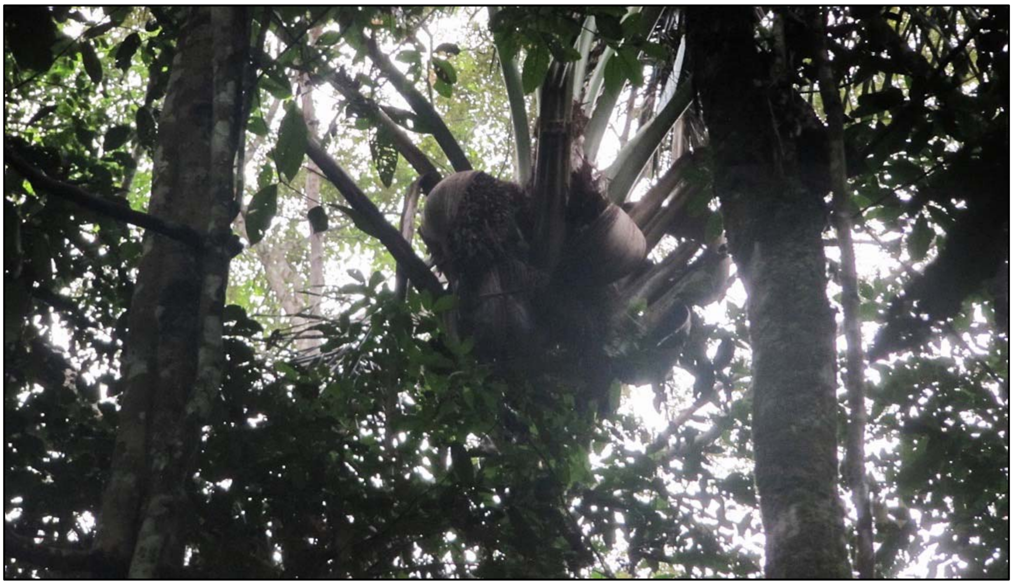


Figure 2.9 Pina swamp forest (above) and maripa palm (below) (photos by S.D).

(3) Palm forest (Figure 2.10): some tall trees present (≥30m) but most do not exceed 20m (e.g. forest papaya (*Cecropia obtusa*) and mope (*Spondias mombin*), which make up a large proportion of *Cebus* and *Sapajus* diets - see van Roosmalen, 1985). The forest floor is covered with ferns and other small foliage but is also abundant in *boegroemaka* (spiky) palms (*Astrocaryum sciophilum*) and/or *Paloeloe* palms (*Phenakospermum guyannese*).

(4) Bamboo patches (Figure 2.11): surrounded by tall trees and or palms, occasionally one or two trees are within the bamboo (*Guadua latifolia*). These dense and continuous patches rarely exceeded 5m and as such were classed as understory in vertical stratification observations.

Figure 2. 10 Palm forest in the Raleighvallen Nature Reserve (photo by S.D).

Figure 2. 11 Bamboo patch in the Raleighvallen Nature Reserve (photo by S.D).

(5) High forest (Figure 2.12): it is possible to distinguish three to four storeys (e.g. Mittermeier & van Roosmalen, 1981; Yoneda, 1984; Fleagle 1999). The understory consists of saplings and undergrowth species, while the lower to middle canopy consists of slender trees. The crowns of emergent trees (≥30m) are wide (e.g. *Ceiba pentandra*) and spread over surrounding 'lower' trees and palms. Epiphytes are common, lianas and vines are less abundant and stilt roots are rare. This type of forest is very rich in species and includes far more edible fruit-producing trees (approximately 331, see Mittermeier & van Roosmalen, 1981) than any other formation.

(6) Low forest: a subcategory of high rainforest that usually does not exceed 20m in height. It is richer in lianas (see Figure 2.8) than high forest, has fewer *boegroemaka* palms and is considered to be a transition between liana forest and high forest or between high forest and mountain savannah forest.

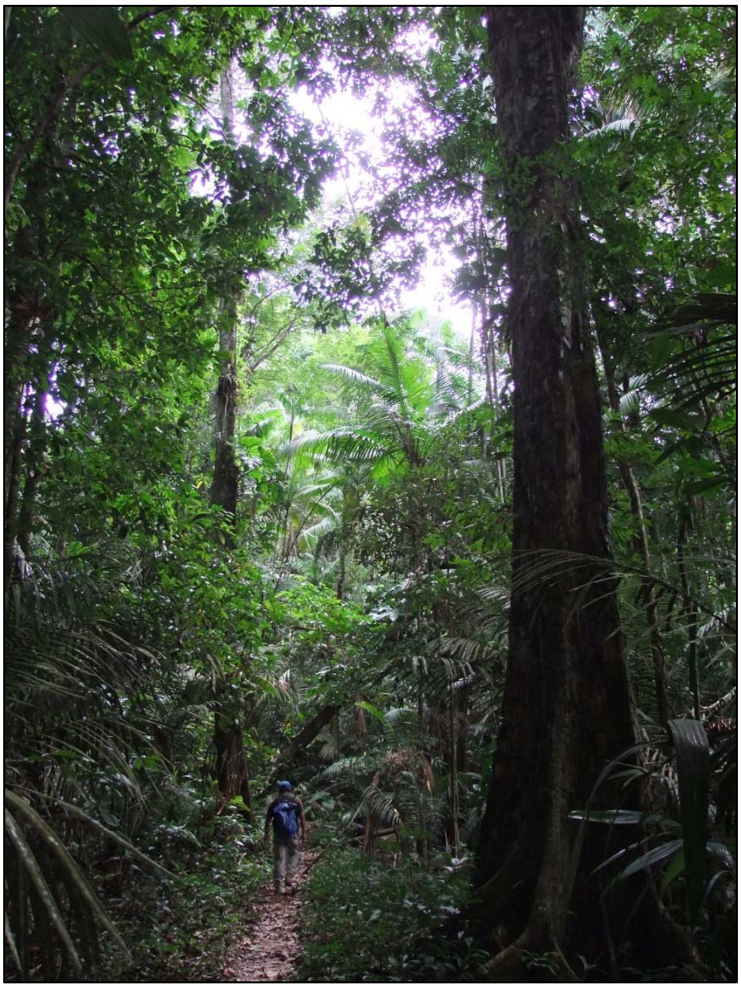


Figure 2. 12 High forest in the Raleighvallen Nature Reserve (photo by S.D).

Quadrats of 2m x 2m (Figure 2.13) were surveyed at 2m perpendicular to the centreline of each trail, and on alternate sides at every 100m point over all trails (six zones and the Voltzberg trail). The following was collected from each quadrat: percentage of ground cover (low and non-woody herbaceous vegetation, vital for squirrel monkeys), ground vegetation height (at mid-point of quadrat), maximum height of rooted vegetation, percentage of canopy cover via a photograph taken directly above observer from the mid-point of the quadrat (Figure 2.13), trees with a circumference at breast height (CBH) of ≥ 30cm (diameter at breast height [DBH] ≥ 10cm) and basal circumference were recorded (Nekaris, Liyanage & Gamage, 2005; Sutherland, 2006), noting the species where possible.

Figure 2.13 2m x 2m quadrat (above) and canopy cover (below) at point 15 in zone B2 (photos by S.D).

Opportunistic data were also collected on the feeding trees utilised by *Sapajus* and *Saimiri* as both include fruits as part of their diet. If more than 3 individuals of either species were encountered feeding in a fruiting tree then a GPS point was taken, the tree was tagged and the following measurements taken (CBH), basal circumference and estimated height. Fruits from the following plant families: *Arecaceae, Moraceae, Burseraceae, Fabaceae/ Mimosaceae, Palmae, Sapotaceae, Lecythidaceae* and *Capparaceae* have previously been identified as important food sources for *Sapajus* (see Mittermeier & van Roosmalen, 1981; van Roosmalen, 1985).

2.4.4 Census methodology - Raleighvallen & Peperpot

Observations took place at the Raleighvallen Nature Reserve from January 2017 to March 2017, between 7:00am and 5:00pm. Observations at Peperpot Nature Park was undertaken during April-May 2017 during opening hours (09.00am – 04.00pm).

Presence/absence data was collected upon visually encountering *Sapajus* or *Saimiri.* An encounter then initiated an attempt to follow the group, recording: start and end time, 5 min scans on vertical stratification (categories following Mittermeier & van Roosmalen, 1981; Yoneda, 1984), species, number of observed individuals, estimated group spread (vertical and horizontal) and minimum distance between individuals of each species when observed in a mixed-species group (measured as the minimum horizontal and vertical distance between *Sapajus* and *Saimiri* – see Smith, Buchanan-Smith, Surridge & Mundy, 2005), and activities (e.g. locomotion, foraging - insect or plant, and substrate usage) so that the context of partitioning and synchrony of behaviours could be evaluated.

Data were also collected on: observer distance to animals, zone (Raleighvallen only – see Figure 2.7), basic weather description, GPS reading upon encounter and end of follow. If the species were not visible but could be identified acoustically, then a GPS point was taken, noting the time, date and zone (Raleighvallen only).

The following was collected upon encountering any of the other 6 sympatric species (either visually or acoustically) within the Raleighvallen study site: start and end time of encounter, GPS reading, trail number, species, number of observed individuals, stratification/forest level occupied (following Mittermeier & van Roosmalen, 1981; Yoneda, 1984), behaviours/activities (e.g. locomotion, foraging - insect or plant, and substrate usage), observer distance, basic weather description, elevation.

Permissions to conduct research at the Raleighvallen Nature Reserve and Peperpot Nature Reserve was granted by the appropriate authorities (see Appendix I). All work carried out abided by the Association for the Study of Animal Behaviour Ethical Guidelines (A.S.A.B, 2012), and was approved by the Psychology Ethics Committee at the University of Stirling, Scotland (see Appendix II).

2.4.5 Data analysis

General descriptive (exploratory) analyses are presented for habitat classifications, primate sightings, mixed-species observations and activity budgets of *Sapajus* and *Saimiri* in single- and mixed-species groups. Group spread was determined as the maximum horizontal (*a*) and vertical distance (*b*) between conspecifics (Waser, 1974; Olupot, Chapman, Waser & Isabirye-Basuta, 1997; Smith et al., 2005). The estimated elliptical area (*e*) of the group was then calculated as $\Pi \text{ x } a \text{ x } b$ (King & Cowlishaw, 2009). Interspecific proximity in mixed-species groups was determined as the minimum horizontal and vertical distance between *Sapajus* and *Saimiri* (Smith et al., 2005).

In order to quantify vertical stratification, I applied Yoneda's (1984) formula:

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

where *i* indicates the types of forest layers (understory=0-5m; lower canopy=5-10m; mid canopy=10-20m; upper canopy=20-30m; emergent=>30m), and f_i and l_i are the respective percentages of utilisation by *Sapajus* and *Saimiri* of forest layer *i*. The possible values of vertical stratification (VS) calculated from the formula range from 0% (complete overlap) and 100% (complete segregation). Mann-Whitney *U* tests were used to examine the differences in vertical stratification between *Sapajus* and *Saimiri* (Field, 2009).

Foraging advantages and shared vigilance (i.e. reduced risk of predation – see Sections 1.2; 1.3) are two of the reasons given for grouping in animals. In order to assess what variables could be contributing to the proportion of foraging and vigilant behaviours observed in single- and mixed-species groups, linear (LM) and linear mixed (LMM) models were developed. The Enter method was adopted to examine the contribution of a range of factors including: species (*Saimiri/Sapajus*); single- or mixed-species scans; group size; date and time; weather (see Chapter 3); and zone (Raleighvallen only – see Figure 2.7). Predictor variables were first examined for collinearity using a Variance Inflation Factor (VIF) test, to which no problematic correlations were identified (i.e. no values exceeded 5; see James, Witten, Hastie & Tibshirani, 2013).

All descriptives, Chi-square and Mann-Whitney *U* tests were conducted in IBM SPSS version 23, and all LMs and LMMs were performed using the software package R (version 3.6.3) in the RStudio environment (R Core Team, 2020; RStudio, 2020 - see code for all R analysis here https://osf.io/kn94r/). Figures were produced using Microsoft Excel 2019.

2.5 Results

2.5.1 Raleighvallen Nature Reserve

2.5.1.1 Habitat Classification

During the study period a total of 155 quadrats were sampled; 20 quadrats for each zone (A1, B1, C1, A2, B2 and C2) with the exception of the existing Voltzberg trail, where 35 quadrats were sampled. Figure 2.14 shows the abundance of each perceived habitat category for all 100m points along trails within the total study area. The proportion of palm forest surveyed was greater than any of the other habitat types. Though bamboo patches were not included in quadrat sampling, their locations were still noted as they are known to be a valuable resource for *Sapajus* (Table 2.3). It should be noted that since the study site was situated close to the Coppename River, the data are biased to some degree based on this proximity and would not necessarily be representative of the entire Reserve. It was for this reason that trails were branched off from the pre-existing perpendicular (to the river) Voltzberg trail, in order to assess the effect of distance from the river (see Figure 2.7).

Table 2.3 *Bamboo patches identified within the total study area (important resource for* Sapajus*).*

Zone / Trail	**GPS coordinates**
A2	N 04° 42.934’ W 056° 12.655’
A2	N 04° 42.991’ W 056° 12.148’
B2	N 04° 42.291’ W 056° 12.595’
B2	N 04° 42.563’ W 056° 12.129’
C2	N 04° 41.508’ W 056° 12.181’
Voltzberg	N 04° 41.085’ W 056° 12.337’

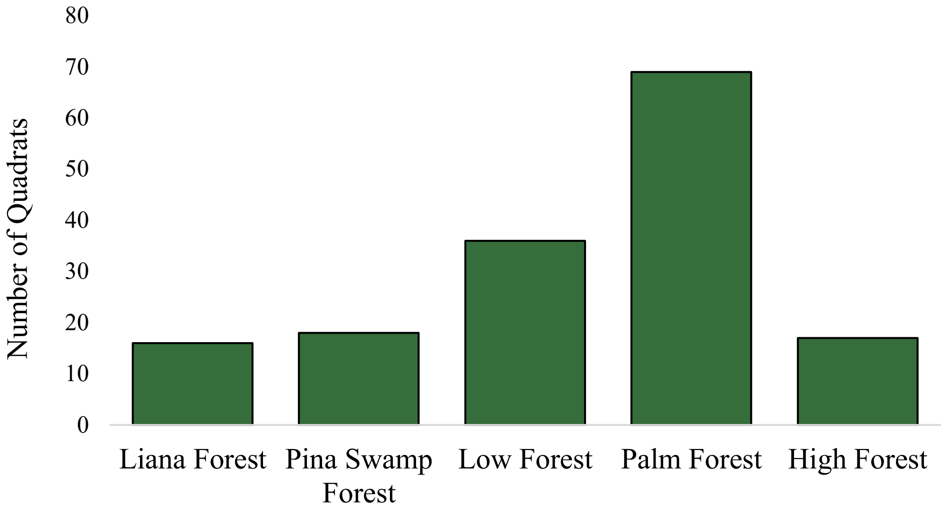


Figure 2. 14 Perceived habitat type for 100m points along trails (*n*=155 quadrats) throughout the study site.

The proportional composition of habitat types changed markedly with distance from the river (see Figures 2.15 and 2.7). The most similar quadrats in terms of perceived vegetation type were those situated in zones C1, B2 and C2. The quadrats in zone A1 were the most different, suggesting increasing habitat homogeneity with distance from the river. The perpendicular Voltzberg trail showed little similarity with zone A1 and varying degrees of similarity with the other transects at greater distances from the river.

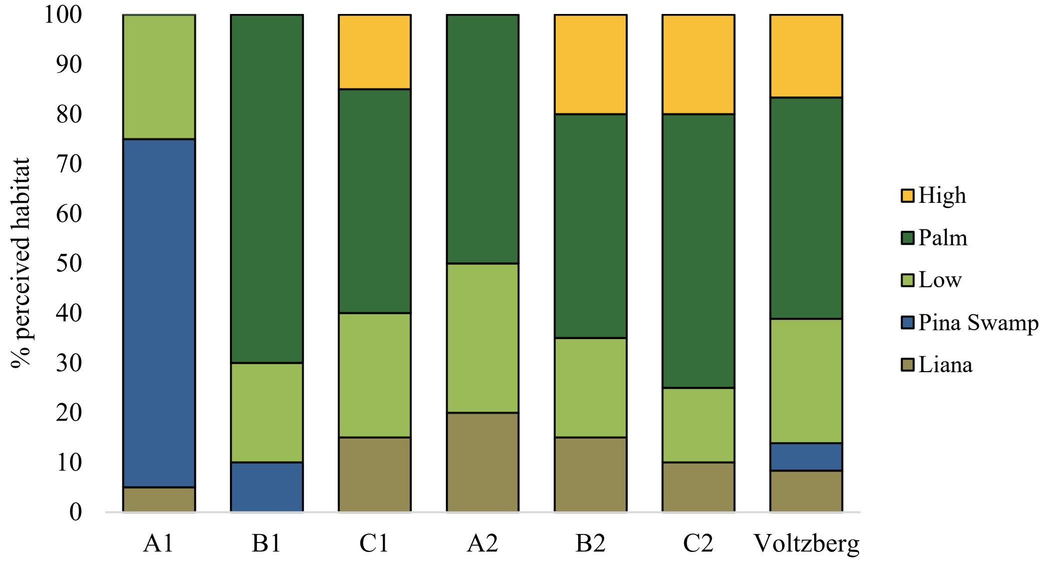


Figure 2.15 The proportion (%) of perceived habitat type (refer to section 2.4.3.2 for more detailed descriptions of habitat classifications) for 100m points along trails (*n*=155 quadrats) throughout the study site (see Figure 2.7 for a map of the study site).

As a physical factor, canopy cover can have a direct effect on the potential for understory growth, which is a useful indicator of where the study species are likely to be located (e.g. *Saimiri* are often observed in dense vegetation / areas with high canopy cover). The programme Image*J* was used to quantify canopy cover from photographs (measured in pixels), by calculating the proportion of plant coverage and openness. Canopy cover was generally greater in zones A2 (*Mdn* = 91; *IQR* = 10), B2 (*Mdn* = 92; *IQR* = 4) and C2 (*Mdn*= 88; *IQR* = 7) than A1 (*Mdn* = 72; *IQR* = 14), B1 (*Mdn*= 80; *IQR* = 7) and C1 (*Mdn*= 81; *IQR* = 15) (see also Figure 2.16), but despite the varying differences in habitat categories (see Figure 2.15), no significant differences were found ($\chi^2 = 3.35$, $p = 0.76$).

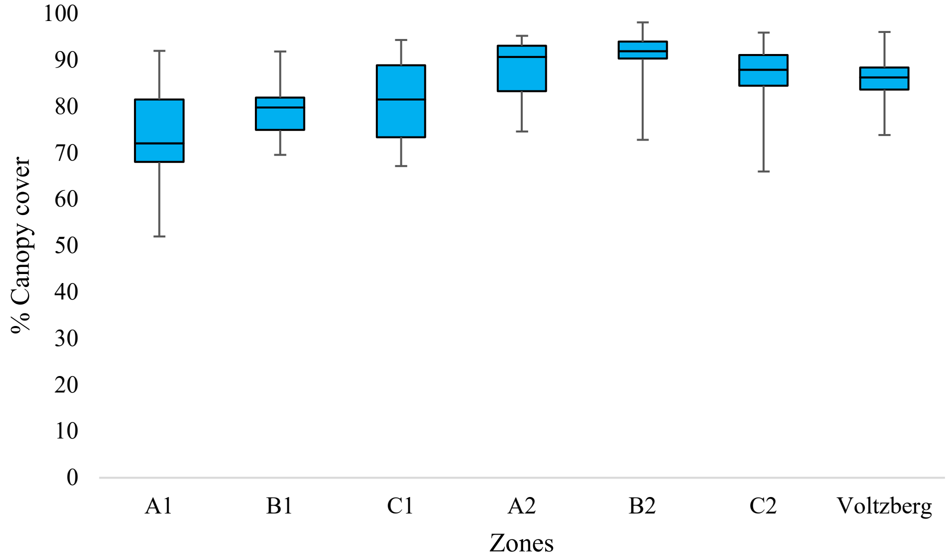


Figure 2.16 Percentage canopy cover for quadrats (*n*=155) along each trail within the study site: **A1** (predominantly pina swamp forest), **B1** (predominantly palm forest), **C1** (predominantly palm forest with some liana, low and high forest), **A2** (palm forest with some liana and low forest), **B2** (predominantly palm forest, with some liana, low and high forest), **C2** (predominantly palm forest, with some liana, low and high forest), **Voltzberg** perpendicular trail (encompasses elements of each of the habitat classifications) see Figure 2.15 for more details on habitat for each trail.

2.5.1.2 Frequency of Primate Sightings

Field primatologists often experience difficulties with identifying individuals, particularly when studying unhabituated arboreal species, such as those found in the Neotropics, and even more so for species that are smaller in size (e.g. *Saguinus* and *Saimiri*) and lack sexual dimorphism (e.g. *Chiropotes, Alouatta, Ateles, Sapajus* or *Cebus*). Consequently, individual identification was not possible for the duration of the study period, nor was it possible to always determine the exact number of individuals observed in an encounter (e.g. if in an area of dense vegetation then possible that some monkeys were out of sight). Due to the small number of encounters in the complete data set for *Sapajus* and *Saimiri* (*n*=83 encounters), it was thought to be more appropriate to present only descriptive statistics using all data points (*n*=number of *Sapajus* encounters; *n*=number of *Saimiri*). Encounter rates were also low for the other primate species: *Saguinus midas* (*n*=16), *Cebus castaneus* (*n*=8), *Chiropotes sagulatus* (*n*=13), *Alouatta macconnelli* (*n*=16) and *Ateles paniscus* (*n*=18).

Each zone (A1, B1, C1, A2, B2, C2) was sampled ten times with the exception of the pre-existing (perpendicular) Voltzberg trail, which was sampled twenty-six times (proportions were calculated in order to account for this imbalance in sampling). This was due to the necessity of utilising the Voltzberg trail in order to access each zone and to counterbalance where walks would begin, so as not to oversample zones closer to the river (e.g. A1 and A2) in the mornings or zones further way from the river in the afternoons (e.g. C1 and C2). Additionally, due to the uncertainty of observing primates on the trails and the short duration of the field study, it was thought preferable to take note of all primate encounters.

Seven of the eight primate species were encountered at the study site (*Pithecia pithecia*) was the only species not encountered during the study period), with the majority of observations occurring in low to high forest and palm forest (see Figures 2.17 and 2.15). Smaller species such as *Saguinus* and *Saimiri* were most often encountered in zones including a larger proportion of understory vegetation (e.g. zone A2: lianas and vines or zone A1: *Pina* swamp forest see Figure 2.15). Whereas larger species such as *Ateles, Alouatta, Cebus, Chiropotes* and *Sapajus* were most dependent on zones predominantly consisting of low to high forest, including palm forest (see Figure 2.15).

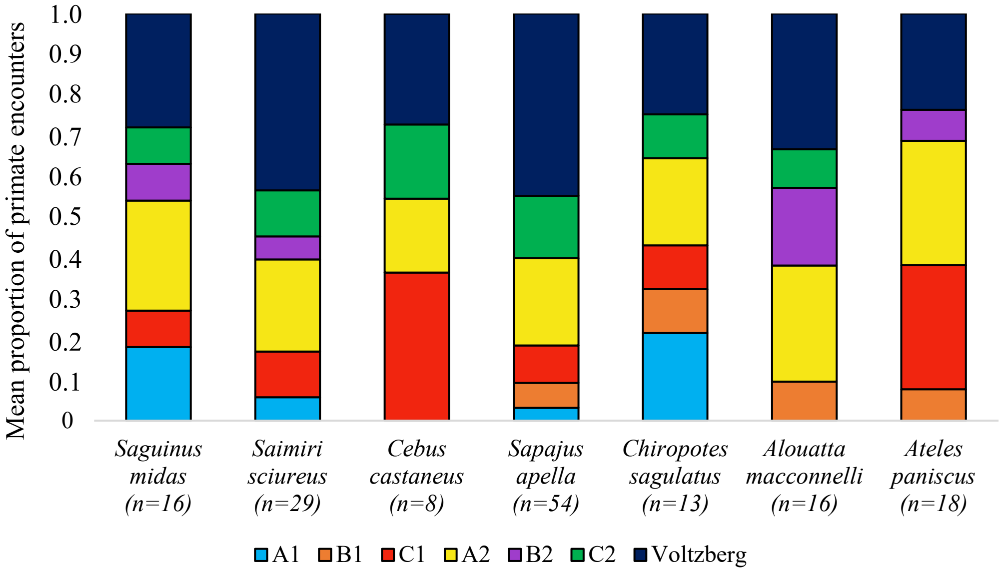


Figure 2.17 Mean proportion of primate encounters across the different trails: **A1** (predominantly pina swamp forest), **B1** (predominantly palm forest), **C1** (predominantly palm forest with some liana, low and high forest), **A2** (palm forest with some liana and low forest), **B2** (predominantly palm forest, with some liana, low and high forest), **C2** (predominantly palm forest, with some liana, low and high forest), **Voltzberg** perpendicular trail (encompasses elements of each of the habitat classifications) see Figure 2.15 for more details on habitat for each trail.

2.5.1.3 Mixed-species Observations

For the purpose of this study, mixed-species groups were considered if *Sapajus* and *Saimiri* were observed ≤20m apart (following Podolsky, 1990) during each five-minute scan (i.e. prerequisite 3 - proximity in time and space – see Figure 1.1). Table 2.4 lists the frequency of primate encounters (single- and mixed-species) observed at the study site. Many of the associations were nothing more than chance encounters of very brief duration, whereas others, especially those involving *Sapajus* and *Saimiri* and to a lesser extent, *Chiropotes* were of longer duration and therefore hold greater ecological significance.

During the study *Saguinus* and *Cebus* were never observed with other monkeys, whereas *Sapajus* were observed with other primate species in 55% of encounters, *Chiropotes* 23% of encounters, *Alouatta* 31% of encounters and *Ateles* for 11% of encounters (see Table 2.4 with frequencies of encounters). The most common associations lasting more than a brief duration involved *Sapajus* and *Saimiri,* followed by *Sapajus* and *Chiropotes.* Groups of *Sapajus* were observed in proximity with *Saimiri* on 15% (*n*=54) of encounters and *Saimiri* with *Sapajus* on 28% (*n*=29) (Table 2.4), with follows lasting between 8 and 57 minutes ($\bar{x}$ =31.25). No interspecific interactions were observed except for one instance, where an individual *Sapajus* lunged in an aggressive manner (non-contact) towards three *Saimiri*, who subsequently moved away. When on the move, both species would travel in the same direction, with *Sapajus* generally leading and *Saimiri* following. Groups of *Sapajus* and *Chiropotes* were encountered together on three occasions, with follows lasting from 6 to 35 minutes ($\bar{x}$ =18.33). Interspecific play behaviour was observed between two individuals, and on two out of the three encounters both species were travelling in the same direction, with *Sapajus* leading on one occasion and *Chiropotes* the other. The most frequent reasons for follows ending were due to losing sight of the monkeys in either dense lianas or bamboo patches and on one occasion because of encountering an active wasps' nest.

Table 2.4 *Frequency of primate encounters observed at the study site, including mixed-species sightings (highlighted in bold) between* Sapajus *and* Saimiri, Chiropotes, Alouatta *and* Ateles*, and* Alouatta-Ateles.

	Saguinus midas	*Saimiri sciureus*	*Cebus castaneus*	*Sapajus apella*	*Chiropotes sagulatus*	*Alouatta macconneli*	*Ateles paniscus*
Saguinus midas	16						
Saimiri sciureus	0	29					
Cebus castaneus	0	0	8				
Sapajus apella	0	**8**	0	54			
Chiropotes sagulatus	0	0	0	**3**	13		
Alouatta macconneli	0	0	0	**4**	0	16	
Ateles paniscus	0	0	0	**1**	0	**1**	18

2.5.1.4 Use of Forest Strata

None of the seven primate species within the study site was ever observed on the ground, and only three (*Saguinus, Saimiri* and *Sapajus*) were observed in the understory layer (see Table 2.5). The other three forest strata were utilised by all seven monkeys, with the exception of *Saguinus* that were never seen in high canopy and *Alouatta* that were never seen in low canopy. *Ateles* and *Chiropotes* were primarily observed in the two highest strata, *Alouatta, Cebus* and *Sapajus* in the middle to upper strata, *Saguinus* in the understory and lower strata, and *Saimiri*, as would be expected of an animal that is known to favour liana forest, was observed more often in the understory.

The data presented in Figure 2.18 show the vertical stratification of *Sapajus* and *Saimiri* for single-species and mixed-species sightings. As noted above, group spread can be described as the elliptical area, and may be related to vertical stratification. The mean estimated elliptical area for *Sapajus* ($\bar{x}$ = 582.19m^2; ±*SE* = 33.32m^2; range = 23.56 – 3141.59m^2) was greater than *Saimiri* ($\bar{x}$ = 464.80 m^2; ±*SE* = 34.19m^2; range = 18.85 – 1696.46m^2), which is expected as *Sapajus* utilised all four forest strata. The percentage of observations at each level was relatively similar for *Sapajus* (Figure 2.18, A) regardless of whether sightings were single-species or mixed-species, and as such no significant differences were found ($p > 0.05$ for all). However, *Saimiri* were observed significantly more in lower ($U = 28.5$, $z = -2.648$, $p = 0.008$, $r = -0.50$) and middle strata ($U = 44.5$, $z = -2.516$, $p = 0.01$, $r = -0.48$) when *Sapajus* were also present (Figure 2.18, B).

Table 2.5 *Proportion of forest strata use for* Saguinus, Saimiri, Cebus, Sapajus, Chiropotes, Alouatta *and* Ateles *(n is the number of encounters). Vertical stratification categorisation follows Mittermeier & van Roosmalen (1981).*

	Vertical Stratification			
Species	**0-5m**	**5-10m**	**10-20m**	**20-30m**
Saguinus (*n*=16)	0.13	0.81	0.06	-
Saimiri (*n*=29)	0.46	0.44	0.09	0.01
Cebus (*n*=8)	-	0.25	0.63	0.12
Sapajus (*n*=54)	0.19	0.42	0.30	0.09
Chiropotes (*n=1*3)	-	0.24	0.38	0.38
Alouatta (*n*=10)	-	-	0.90	0.10
Ateles (*n*=17)	-	0.06	0.53	0.41

Using Yoneda's (1984) formula, the vertical segregation between *Sapajus* and *Saimiri* was quantified at 49.3%. This falls within the range of values in other studies of primate mixed-species groups (e.g. 47.3% (primary forest), 76.9% (secondary forest): Yoneda, 1984; 65.5% Buchanan-Smith, 1999a; 56.8%: Prescott, 1999). Horizontal spread accounted for a significant amount of the variation in vertical spread in terms of maximum intraspecific spread (*Sapajus* $R^2 = 0.036$, $F(1,290) = 10.892$, $p \leq 0.001$; *Saimiri* $R^2 = 0.044$, $F(1,160) = 7.387$, $p = 0.007$) and minimum interspecific distance ($R^2 = 0.202$, $F(1, 55) = 13.702$, $p \leq 0.001$).

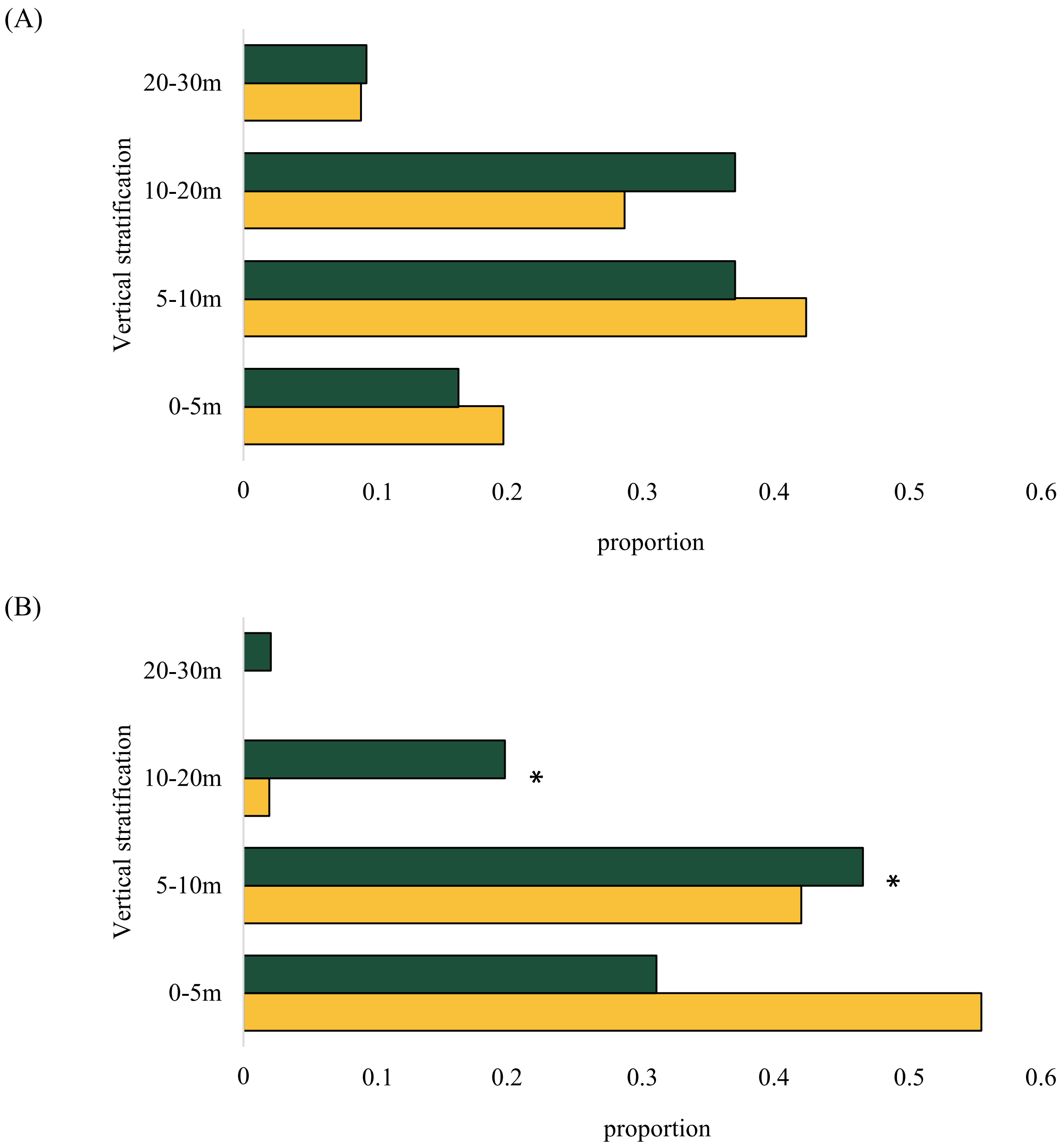


Figure 2.18 Use of forest strata for (A) *Sapajus* (*n*=235 scans); (B) *Saimiri* (*n*=107 scans); mixed scans (*n*=56). An asterisk (*) indicates a significant difference between mixed-species (green bars) and single-species (yellow bars) sightings. Vertical stratification categorisation follows Mittermeier & van Roosmalen (1981).

2.5.1.5 Activity Budgets

Behavioural data are only presented from encounters with *Sapajus* and *Saimiri*, as other primate species would generally flee upon encountering observers. Overall, both species showed little variation in their behaviours regardless of whether they were observed as single-species or mixed-species. However, *Sapajus* appeared to be less vigilant and forage more when *Saimiri* were present (see Figure 2.19 A), and *Saimiri* were observed to forage more and play less when *Sapajus* were present (see Figure 2.19 B). Linear mixed models (LMM) were developed to examine whether the proportion of foraging and vigilance observed were influenced by factors such as species (*Sapajus* or *Saimiri*), whether *Sapajus* or *Saimiri* were in single- or mixed-species groups, and group size. Random factors such as date and time at start of scan, zone (A1, B1, C1, A2, B2, C2 and Voltzberg) and weather were controlled for in the models, however they explained only a small proportion of the variance (see Tables 2.6; 2.7).

An LMM identified a significant difference in proportion foraging when compared with a null model ($F_{3,284}$=14.533, p<0.0001). The full model (see Table 2.6) indicates that proportion foraging was higher in *Sapajus* compared with *Saimiri* and that overall proportion foraging was lower in mixed-species groups compared to single-species. Group size was not found to be a significant contributor to the proportion of vigilance observed (see Table 2.6). Post-hoc pairwise comparisons using the Bonferroni correction indicated that proportion foraging in *Saimiri* single-species ($\bar{x}$=0.288, SE=0.064) scans were significantly lower than for *Sapajus* single-species ($\bar{x}$=0.389, SE=0.064, t= -4.384, p<0.001). Similarly, in mixed-species scans the proportion of foraging was significantly lower in *Saimiri* ($\bar{x}$=0.193, SE=0.077) than in *Sapajus* ($\bar{x}$=0.295, SE=0.076, t= -4.384, p<0.001). However, no significant differences were found based on whether the monkeys were observed in single- or mixed-species groups or for group size (see Table 2.6).

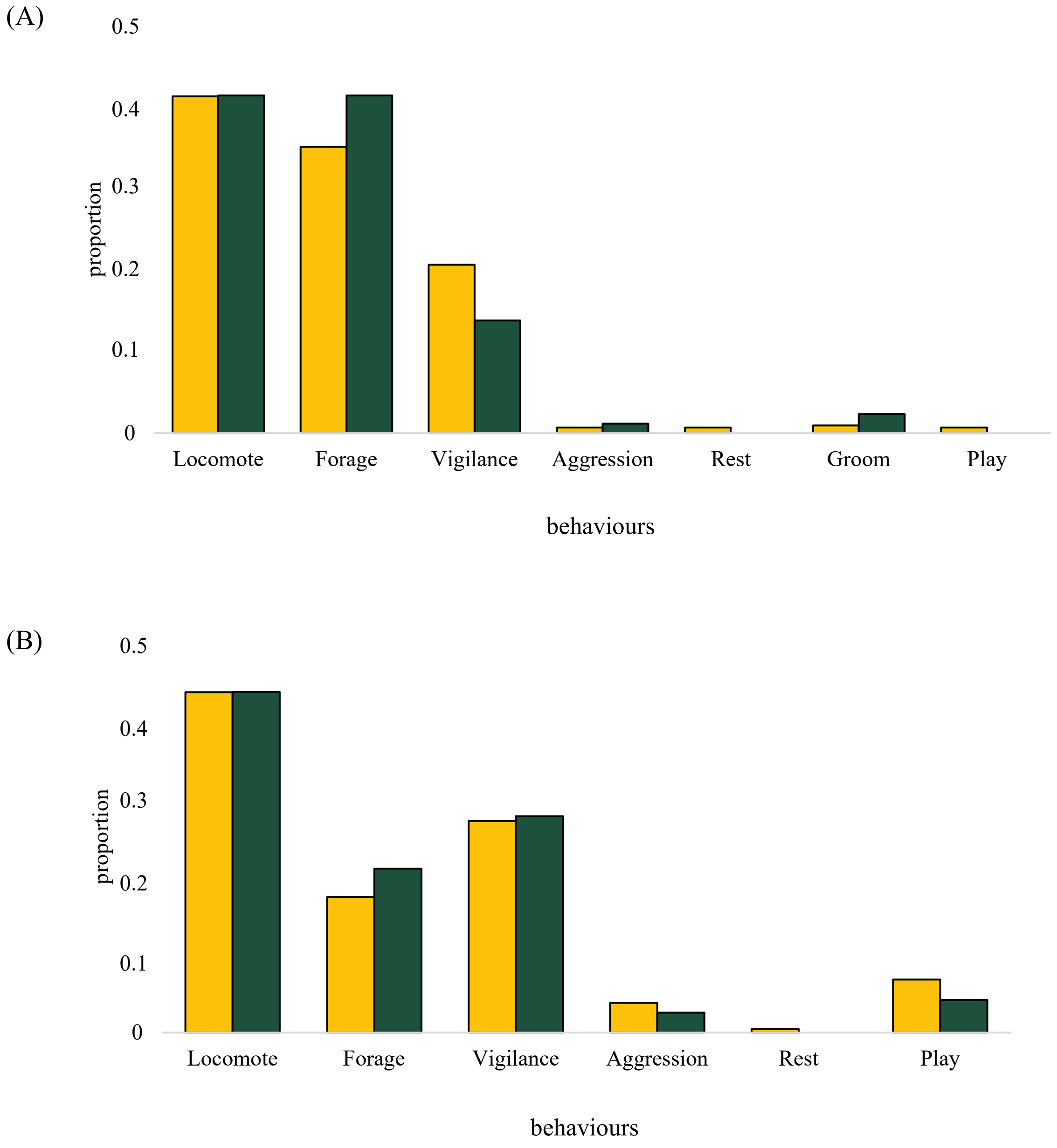


Figure 2.19 Activity budgets for (A) *Sapajus* (*n*=235), (B) *Saimiri* (*n*=107); mixed (*n*=56). Green bars represent mixed-species sightings and yellow bars for single-species sightings.

An LMM identified a significant difference in proportion vigilance when compared with a null model ($F_{3,253}$=14.531, p<0.0001), weather was removed as it created a singular fit, and did not contribute to the variance (~0%) in the model. The full model indicates that proportion vigilance was lower in *Sapajus* compared with *Saimiri* and that overall proportion vigilance was lower in mixed-species groups compared to single-species (see Table 2.7). Group size was not found to be a significant contributor to the proportion of vigilance observed (see Table 2.7). Post-hoc pairwise comparisons using the Bonferroni correction indicated that the proportion of vigilant behaviours observed in *Saimiri* single-species scans ($\bar{x}$=0.146, SE=0.016) and mixed-species scans ($\bar{x}$=0.090, SE=0.021) were significantly higher compared to *Sapajus* single-species ($\bar{x}$=0.075, SE=0.0142, t=5.945, p<0.0001) and mixed-species scans ($\bar{x}$=0.019, SE=0.019, t=5.945, p<0.0001). However, no significant differences were found between *Saimiri* single-species and mixed-species scans, nor between *Sapajus* single-species and mixed-species.

Table 2.6 *Linear mixed model (LMM) outlining contributing factors (predictor variables) to* Sapajus *and* Saimiri *single-species and mixed-species groups' proportion observed foraging, controlling for date and time, zone (A1,B1,C2,A2,B2,C2,Voltzberg) and weather (random factors), based on a total of 396 scans (*Sapajus*=235;* Saimiri*=105; mixed-species =56).*

Random factors	**Variance**	**SD±**		
Date-time	0.083	0.289		
Zone	0.013	0.116		
Weather	0.0007	0.142		
Predictor variables	**Estimate**	**SE**	***t***	***P***
Intercept (species=*Saimiri*; group=single-species, group size)	0.361	0.069	5.203	0.003
Species (*Sapajus*)	0.102	0.023	4.434	<0.0001
Group (mixed-species)	-0.094	0.056	-1.687	0.092
Group size (species=*Sapajus*; group= mixed-species)	-0.010	0.006	-1.682	0.093
Full model $F_{3,284}$=14.533, p<0.0001				

Table 2.7 *Linear mixed model (LMM) outlining contributing factors (predictor variables) to* Sapajus *and* Saimiri *single-species and mixed-species groups' proportion observed vigilant, controlling for date and time, zone (A1,B1,C2,A2,B2,C2,Voltzberg) and weather (random factors), based on a total of 396 scans (*Sapajus*=235;* Saimiri*=105; mixed-species =56).*

Random factors	**Variance**	**SD±**		
Date-time	0.0099	0.099		
Zone	0.0001	0.116		
Predictor variables	**Estimate**	**SE**	***t***	***P***
Intercept (species=*Saimiri*; group=single-species, group size)	0.139	0.021	6.673	<0.0001
Species (*Sapajus*)	-0.072	0.012	-6.018	<0.0001
Group (mixed-species)	-0.056	0.021	-2.670	0.008
Group size (species=*Sapajus*; group= mixed-species)	0.001	0.002	0.435	0.664
Full model $F_{3,253}$=14.531, p<0.0001				

2.5.2 Peperpot Nature Park

Only three (*Sapajus, Saimiri* and *Chiropotes*) of the eight Suriname monkeys were encountered during the study period (see section 2.4.2). One troop of *Sapajus* (estimated 8 individuals) and *Saimiri* (estimated 15-20 individuals) were known to inhabit the area surrounding the main Mopentibo trail, however, individual identification (beyond alpha males) was not possible for the duration of the study. *Sapajus* were observed in proximity with *Saimiri* on 92% (n = 13) of encounters and *Saimiri* with *Sapajus* on 30% (n = 44), with the duration of follows lasting between 7 and 31 minutes ($\bar{x}$ = 16.83).

Given the higher frequencies of association during *Sapajus* encounters, it is of interest to compare the ecological niches occupied by both species in order to establish how similarities and/or differences in these, permit their coexistence. Figure 2.20 shows the vertical stratification of *Sapajus* and *Saimiri* for single-species and mixed-species sightings. The mean estimated elliptical area for *Sapajus* ($\bar{x}$ = 126.26m^2; ±SE = 12.98m^2; range = 1.57 – 612.61m^2) was greater than *Saimiri* ($\bar{x}$ = 95.80 m^2; ±SE = 6.19m^2; range = 3.14 – 589.05m^2). The percentage of observations at each level was relatively similar for *Sapajus* (Figure 2.20, A) regardless of whether sightings were single-species or mixed-species, and as such no significant differences were found (p>0.05 for all strata). Similarly, the percentage of observations between strata were relatively similar for *Saimiri*, with the exception of the middle canopy where interestingly, they were observed significantly more ($U = 192.5$, $z = -2.296$, $p = 0.022$, $r = -0.30$) when *Sapajus* were not present (Figure 2.20, B). This unexpected result may be due to the majority of mixed-species observations occurring amongst bamboo patches (*Guadua* sp.). Furthermore, neither *Sapajus* nor *Saimiri* were ever observed on the ground nor in the emergent canopy.

Using Yoneda's (1984) formula, the vertical segregation between *Sapajus* and *Saimiri* was quantified at 17.07%. This falls lower than the range of values found at Raleighvallen and in other studies of primate polyspecific associations (see section 2.5.1.4 and Yoneda, 1984; Buchanan-Smith, 1999a; Prescott, 1999), but this greater amount of overlap is likely due to a smaller habitat range and generally lower height of the overall canopy (i.e. secondary forest growth). Horizontal spread accounted for a significant amount of the variation in vertical spread in terms of maximum intraspecific spread (*Sapajus* $R^2 = 0.093$, $F(1,99) = 10.081$, $p = 0.002$; *Saimiri* $R^2 = 0.140$, $F(1,217) = 35.214$, $p \leq 0.001$) but not for minimum interspecific distance ($R^2 = 0.002$, $F(1, 40) = 0.069$, $p = 0.794$).

Behavioural data are presented in Figure 2.21. Overall, both *Sapajus* and *Saimiri* show little variation in their behaviours regardless of whether they were encountered in single-species or mixed-species groups. Interestingly we are seeing almost the opposite of findings from Raleighvallen (see section 2.5.1.5), whereby *Sapajus* and *Saimiri* appear to be more vigilant and forage less when the other species were present (see Figure 2.21). Linear mixed models (LMM) were developed to examine whether the proportion of foraging and vigilance observed at Peperpot were influenced by factors such as species (*Sapajus* or *Saimiri*), whether *Sapajus* or *Saimiri* were in single-species or mixed-species groups, and group size. Random factors such as date and time at start of scan, and weather were controlled for in the models (see Tables 2.8; 2.9).

An LM identified a significant difference in proportion foraging when compared with a null model ($F_{3,314}$=20.28, p<0.0001). Random factors date and time at start of scan, and weather were removed from the model as they were found to be redundant as covariance parameters (test statistics and confidence intervals could not be computed, and they explained ~0% of the variance). The full model (see Table 2.8) indicates that proportion foraging was higher in *Sapajus* compared with *Saimiri* and that overall proportion foraging was lower in mixed-species groups compared to single-species. Group size was not found to be a significant contributor to the proportion of vigilance observed (see Table 2.8). Post-hoc pairwise comparisons using the Bonferroni correction indicated that proportion foraging in *Saimiri* single-species scans ($\bar{x}$=0.132, SE=0.015) was significantly lower than for *Sapajus* single-species ($\bar{x}$=0.293, SE=0.023), t= -6.637, p<0.0001). Similarly, in mixed-species scans the proportion of foraging was significantly lower in *Saimiri* ($\bar{x}$=0.025, SE=0.027) than in *Sapajus* ($\bar{x}$=0.185, SE=0.027, t= -6.637, p<0.0001). The proportion of foraging observed in both species was significantly lower in mixed-species scans compared to single species (t=3.593, p=0.003). However, group size was not found to have a significant impact on the proportion of foraging observed (see Table 2.8).

An LMM identified a significant difference in proportion vigilance when compared with a null model ($F_{3,236}$=8.882, p<0.0001). The full model (see Table 2.9) indicates that proportion vigilance was lower in *Sapajus* compared with *Saimiri* and that overall proportion vigilance was lower in mixed-species groups compared to single-species. Group size was not found to be a significant contributor to the proportion of vigilance observed (see Table 2.8). Post-hoc pairwise comparisons using the Bonferroni correction indicated that the proportion of vigilant behaviours observed in *Saimiri* single-species scans ($\bar{x}$=0.214, SE=0.015) was significantly higher compared to *Sapajus* single-species scans ($\bar{x}$=0.147, SE=0.020, t=3.702, p=0.002). The same pattern was observed in mixed-species scans, (*Saimiri*: $\bar{x}$=0.142, SE=0.028; *Sapajus*: $\bar{x}$=0.075, SE=0.027, t=3.702, p=0.018). No significant differences were found in the proportion of vigilance observed in *Saimiri* single-species and mixed-species scans nor between *Sapajus* single-species and mixed-species. Though in the overall model proportion vigilance was significantly lower in mixed-species groups compared to single-species groups (see Table 2.9). Group size was not found to be a significant contributor to the proportion of vigilance observed (see Table 2.9).

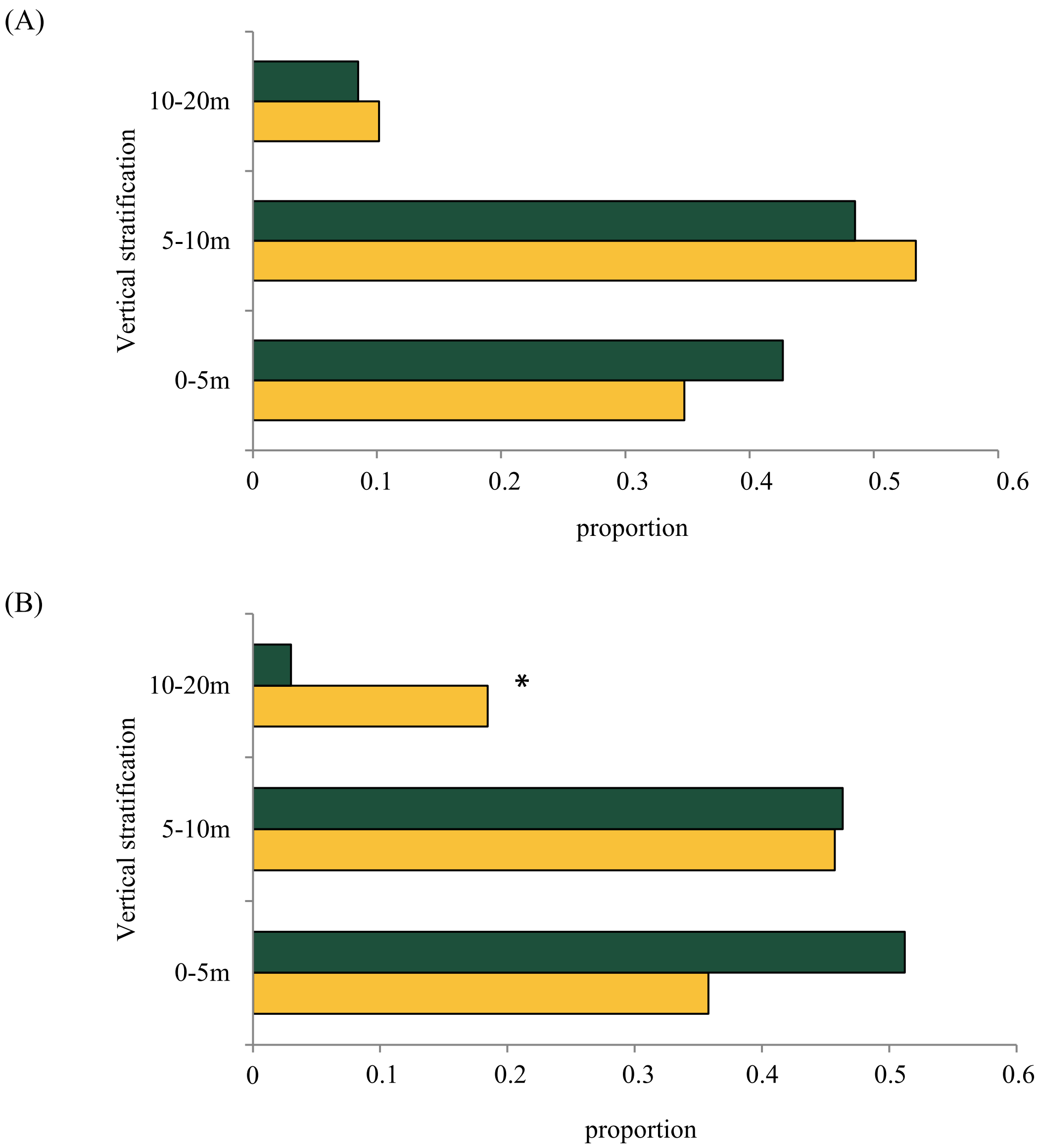
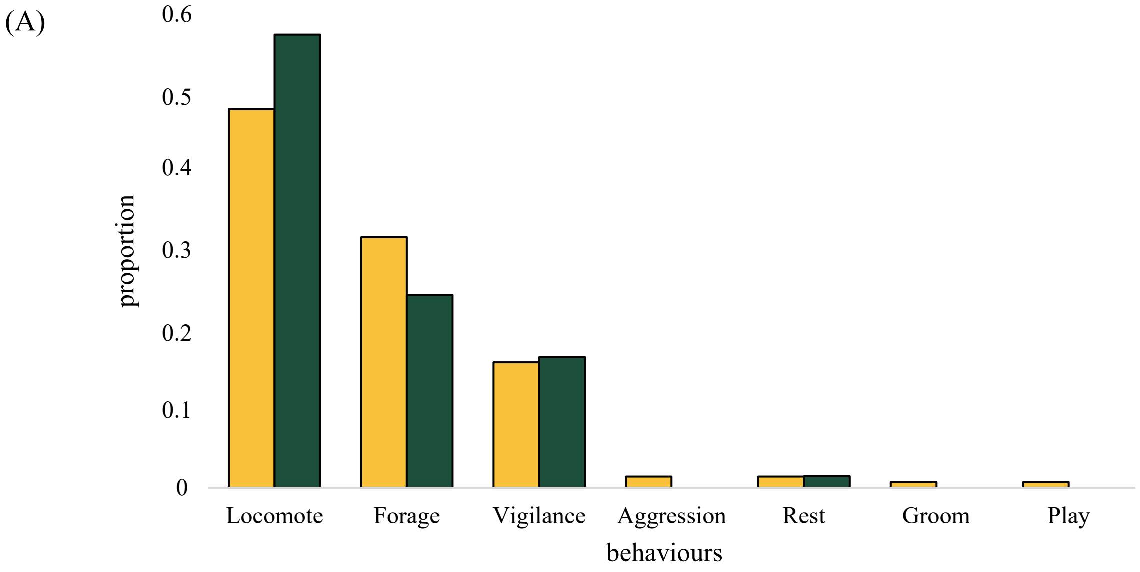


Figure 2.20 Use of forest strata for (A) *Sapajus* (*n*=59 scans); (B) *Saimiri* (*n*=178 scans); mixed scans (*n*=41). An asterisk (*) indicates a significant difference between mixed-species (green bars) and single-species (yellow bars) sightings. Vertical stratification categorisation adapted from Mittermeier & van Roosmalen (1981).



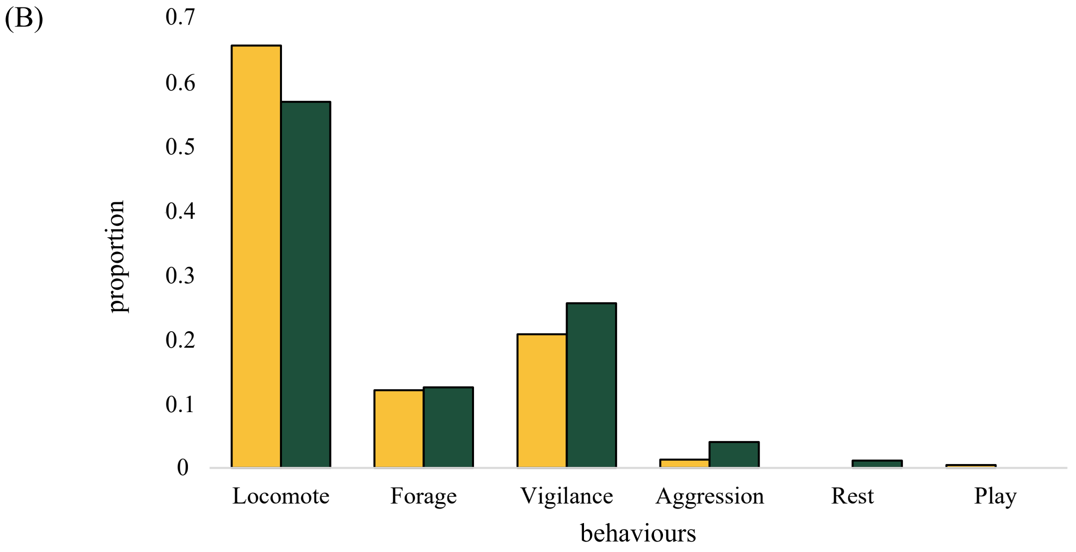


Figure 2.21 Activity budgets for (A) *Sapajus* (*n*=59), (B) *Saimiri* (*n*=178); mixed (*n*=41). Green bars represent mixed-species sightings and yellow bars for single-species sightings.

Table 2.8 *Linear model (LM) outlining contributing factors (predictor variables) to* Sapajus *and* Saimiri *single-species and mixed-species groups' proportion observed foraging at the Peperpot Nature Park, based on 277 scans (*Sapajus*=59;* Saimiri*=177; mixed-species =41).*

Predictor variables	**Estimate**	**SE**	***t***	***P***
Intercept (species=*Saimiri*; group=single-species, group size)	0.173	0.031	5.521	<0.0001
Species (*Sapajus*)	0.161	0.024	6.720	<0.0001
Group (mixed-species)	-0.107	0.029	-3.706	<0.001
Group size (species=*Sapajus*; group= mixed-species)	-0.007	0.005	-1.324	0.186
Full model $F_{3,314}$=20.28, p<0.0001				

Table 2.9 *Linear mixed model (LMM) outlining contributing factors (predictor variables) to* Sapajus *and* Saimiri *single-species and mixed-species groups' proportion observed vigilant at the Peperpot Nature Park, controlling for date and time and weather (random factors), based on a total of 277 scans (*Sapajus*=59;* Saimiri*=177; mixed-species =41).*

Random factors	**Variance**	**SD±**		
Date-time	0.1327	0.115		
Weather	0.0002	0.016		
Predictor variables	**Estimate**	**SE**	***t***	***P***
Intercept (species=*Saimiri*; group=single-species, group size)	0.220	0.029	7.591	<0.0001
Species (*Sapajus*)	-0.068	0.018	-3.756	<0.001
Group (mixed-species)	-0.072	0.028	-2.543	0.012
Group size (species=*Sapajus*; group= mixed-species)	-0.001	0.005	-0.202	0.840
Full model $F_{3,236}$=8.882, p<0.0001				

2.6 Discussion

Applying a combined field-captive approach to research can provide valuable and complementary information that helps us to: (1) better understand an animal's behavioural ecology in the wild; (2) formulate and test hypotheses under controlled conditions in captivity; (3) design and appropriately interpret studies in captivity; (4) suggest avenues for future research (e.g. the need for longitudinal research in the wild as well as in captivity); and (5) help guide conservation efforts *in situ* and via public engagement with science. The ecological information (e.g. habitat and natural behaviours) gathered from wild populations can help to improve the ecological validity of captive research and provide context for the results of captive behavioural studies (e.g. Buchanan-Smith & Hardie, 1997; Dawkins, 1998; Leonardi et al., 2010; Zimbler-DeLorenzo & Stone, 2011; Mellor & Beausoleil, 2015; Keulartz, 2015 and see Chapter 3). This Chapter highlights some interesting points on the behavioural ecology of *Sapajus* and *Saimiri* in the wild. For instance, the variation in vertical stratification and activity budgets observed at the two study sites (see Table 2.10). Furthermore, on one of the *Saimiri* follows in Raleighvallen I recorded the monkeys leaping (one by one) from one tree into another (still within the low to understory sections), an observation that was also noted by Baldwin (1985). Information such as this on the locomotion of *Saimiri* would therefore be useful when considering enclosure design in captivity in order to encourage more natural movement such as leaping.

Table 2.10 *Summary of main findings in Chapter 2.*

	Raleighvallen Nature Reserve	Peperpot Nature Park
Habitat	Primary Forest	Secondary Forest (previously a plantation)
Max. canopy height primates observed (*approx.*)	20-30m	10-20m
Primates encountered	7 of 8 (*Saguinus, Saimiri, Cebus, Sapajus, Chiropotes, Alouatta* and *Ateles*)	3 of 8 (*Saimiri, Sapajus* and *Chiropotes*)
Sapajus encounters	*n* = 54	*n* = 13
with *Saimiri*	15%	92%

Table 2.10 *continued.*

Saimiri encounters with *Sapajus*	*n* = 29 28%	*n* = 44 30%
Vertical stratification	*Sapajus* were observed across their vertical space, with higher proportions in the mid to lower stories of the canopy (see Figure 2.18, A).	*Sapajus* were observed mostly at heights of 0-5m and 5-10m. They were observed at lower heights more when *Saimiri* were present, but at higher levels significantly more when in single-species (see Figure 2.20, A).
	Saimiri were observed across the vertical space but mostly in the understory and lower levels of the canopy. They were only ever observed in high canopy (20-30m) when *Sapajus* were also present.	*Saimiri* were observed across the vertical space but more so between heights 5-10m. They were at higher levels more often when *Sapajus* were not present, and lower levels (0-5m) when *Sapajus* were present (see Figure 2.20, B).
Activity budgets	An LMM indicated that proportion foraging observed in *Sapajus* was higher compared with *Saimiri* and that overall proportion foraging was significantly lower in mixed-species groups compared to single-species groups (see Table 2.6). Group size was n.s.	An LM indicated that proportion foraging observed in *Sapajus* was higher compared with *Saimiri* and that overall proportion foraging was significantly lower in mixed-species groups compared to single-species groups (see Table 2.8). Group size was n.s.
	An LMM indicated that the proportion of vigilance observed was significantly lower in *Sapajus* compared with *Saimiri* and that overall proportion vigilance was significantly lower in mixed-species groups compared to single-species groups (see Table 2.7). Group size was n.s.	An LMM indicated that the proportion of vigilance observed was significantly lower in *Sapajus* compared to *Saimiri* and that overall proportion vigilance was significantly lower in mixed-species groups compared to single-species groups (Table 2.9). Group size was n.s.
Double benefits hypothesis	Partial support for Pulliam's double benefits hypothesis (i.e. reduced vigilance, but foraging cost in mixed-species group)	

Previous research in the interior regions of Suriname (including the Raleighvallen Nature Reserve) have been described as having diverse and relatively undisturbed primate communities (e.g. Fleagle & Mittermerier, 1980; Mittermeier & van Roosmalen, 1981; Norconk & Kinzey, 1994). During the present study seven out of the eight known species of Suriname primates were encountered (though did not observe *Pithecia*) at the Raleighvallen Nature Reserve. Encounter rates for *Sapajus* and *Saimiri* were similar to frequencies reported in previous studies at Raleighvallen (Table 2.11), however the percentage of sightings in mixed-species groups were much lower. Furthermore, the frequency of encounters with other primate species (*Saguinus, Cebus, Chiropotes, Alouatta* and *Ateles*) were also comparatively low (see Mittermeier & van Roosmalen, 1981). In contrast, Peperpot Nature Park and the surrounding forest areas are situated closer to the coast, where human settlements are more prevalent, and as such, primate communities are more prone to anthropogenic disturbance. While *Alouatta* and *Pithecia* have been observed in Peperpot in the past (A. Vreedzaam, personal communication, April 3, 2017), only three species of primates were encountered during the study period (*Sapajus*. *Saimiri* and *Chiropotes*). *Sapajus* were sighted less frequently here (*n*=13), with *Saimiri* present for 92% of encounters, whereas *Saimiri* sightings were greater (*n*=44), with a lower percentage (30%) of encounters where *Sapajus* were also present.

Table 2.11 *Frequency of mixed-species associations between* Sapajus *and* Saimiri *in the Raleighvallen Nature Reserve reported from the present study and existing literature.*

Species	***n* encounters**	**% of sightings in association**	**Reference**
Sapajus (with *Saimiri*)	76	45	Mittermeier & van Roosmalen (1981)
	50	58	Fleagle & Mittermeier (1981)
	N/A	58	Boinski, Quatrone & Swartz (2000)
	54	**15**	**Present study (2017)**
Saimiri (with *Sapajus*)	28	100	Mittermeier & van Roosmalen (1981)
	30	97	Fleagle, Mittermeier & Skopec (1981)
	N/A	~30	Boinski, Quatrone & Swartz (2000)
	29	**28**	**Present study (2017)**

Considerable variation was found in both the habitat structure between zones, and at varying distances from the Coppename River. The zones closet to the river were dominated by either *Pina* palms (*Euterpe oleracea*) (A1) or other palm forest species (e.g. *Astrocaryum sciophilum* or *Attaleae maripa*) (B1) with a variable herb layer and several semi-permanent watercourses (e.g. creeks and swamp marshes). Whilst this habitat formation is not particularly rich within the Raleighvallen study site, several of the primate species were observed there (*Saguinus, Saimiri, Sapajus* and *Chiropotes*), possibly for foraging opportunities or simply to pass through into another forest type. Zones further away from the river (C1, A2, B2 and C2) had a higher proportion of lianas, low forest and high forest compared to those closer to the river as well as a higher mean percentage canopy cover (≥80%, see Figure 2.17). As may be expected, there were also more sightings of larger species such as *Ateles* and *Alouatta* here compared to zones closer to the river. Furthermore, zones that were more inland (C1, B2 and C2) were found to be most similar in terms of habitat types (Figure 2.16), which suggests increasing habitat homogeneity with distance from the river.

The study of spatial ecology is important, as it can affect foraging opportunities, encounters with competitors and predators alike, in addition to social interactions (e.g. reproductive opportunities). According to accepted ecological theory, closely related species are not able to coexist without inter-specific competition, which can result in either local extinction or character displacement (see Schoener, 1988; Keddy, 1989; Smith et al., 2005). Therefore, in a region that is both small yet dense in forest fruits (see Figure 2.4) it is interesting that it has such a diverse primate community (including two species of capuchins), which would appear to contradict this principle. Previous research investigating habitat utilization and niche separation in sympatric Neotropical primate communities (Hladik & Hladik, 1969; Hladik et al., 1971; Hladik, 1975; Klein & Klein, 1973, 1975; Izawa, 1975, 1976; Mittermeier & van Roosmalen, 1981; Terborgh, 1983; Buchanan-Smith, Hardie, Caceres & Prescott, 2000; Pinheiro, Ferrari & Lopes, 2011) have found that while there are overlaps in diet (e.g. during seasons when highly nutritious fruit species are abundant), each monkey species has their own specialist diet (especially during periods of food scarcity), thereby adopting different ecological niches. For instance, all of the Suriname primates are known to incorporate fleshy soft-pulp fruits as part of their diet (Mittermeier & van Roosmalen, 1981; Boinski, 2002), but some will also include arthropods, small vertebrates, young leaves or gums and saps (see Figure 2.6).

As well as diet, another aspect that we can look at in terms of niche partitioning is where in the canopy the monkeys are located, especially when the study subjects in question are all arboreal. For example, it is apparent in the present study that the monkeys utilised different forest strata, with smaller species (*Saguinus* and *Saimiri*) mostly occupying the understory (0-5m) and lower levels (5-10m) of the canopy, medium (*Cebus, Sapajus* and *Chiropotes*) to large (*Alouatta* and *Ateles*) species mostly occupying the middle (10-20m) to upper levels (20-30m) of the canopy (Table 2.5). Therefore, body size appears to be a critical factor in the structure of sympatric primate communities as it not only constrains positional behaviour, but also foraging techniques and strategies against predators (Gautier-Hion, 1978; Struhsaker, 1978; MacKinnon & MacKinnon, 1980; Terborgh, 1983; Buchanan-Smith, 1999a). This pattern of vertical segregation (e.g. larger species in higher canopy and smaller species in lower canopy) is well documented in the published literature, though it is important to note that different measures for stratification of the forest are reported due to local variants in both forest type and maximum (emergent) heights (Klein & Klein, 1973, 1975; Mittermeier & van Roosmalen, 1981; Buchanan-Smith et al., 2000; Pinheiro et al., 2011). Despite the smaller number of data points, and sampling in a different area of the Raleighvallen site, the proportion of heights for observed species were not too dissimilar to the findings of Mittermeier and van Roosmalen (1981).

Thus, vertical segregation between sympatric primate species is arguably a primary consequence of their ecological, behavioural, and morphological adaptations, which consequently orients these monkeys towards particular strata in the canopy, and so enables their co-existence. Furthermore, vertical segregation along with difference in body size and dietary overlap has been found to play an important role in the formation of mixed-species groups. For instance, previous research on tamarin troops has shown that species with greater dietary overlap (e.g. *Saguinus fuscicollis* and *S. mystax*) tend to have better group stability than those with less dietary overlap (e.g. *S. fuscicollis* and *S. imperator*) (43%: Terborgh, 1983; 80-85%: Norconk, 1986; Peres, 1993b; Buchanan-Smith, 1999a). However, Cords (1990a) study of mixed-species groups of red-tailed monkeys (*Cercopithecus ascanius*) and blue monkeys (*C. mitis*) in East Africa found that they were observed together less at the Kibale site, where dietary overlap was lower compared to the Kakemega site, which supports the notion that the environment and perhaps seasonal variation can impact on the stability of mixed-species groups (Noë & Bshary, 1997; Chapman & Chapman, 2000b). Similarly, Fleagle et al. (1981) found that mixed-species groups of *Sapajus* and *Saimiri* were less frequent during the months October-July (presumably when there was less dietary overlap), compared to June-September. This may also account for the low frequency of mixed-species observations during the present studies.

As discussed in Chapter 1, the two main proposed adaptive functions for the formation of mixed-species associations are (1) foraging advantages and (2) reduced risk of predation (though these benefits are not necessarily mutually exclusive). For example, *Sapajus* flushing out insects to both higher levels of the forest, facilitating their capture by birds (Terborgh, 1990), and lower levels, facilitating their capture by *Saimiri* provides one example of a foraging benefit (Fleagle et al., 1981). This may also provide an explanation as to why *Saimiri* in Raleighvallen were observed in higher levels of the canopy (though still below *Sapajus*) more frequently when *Sapajus* were also present compared with single-species observations (Table 2.10). Furthermore, the LMM (see Table 2.6) identified that *Sapajus* foraged more than *Saimiri* (foraging benefit), but that overall foraging was lower in mixed-species groups compared to single-species groups, which could indicate that there is a foraging cost to forming mixed-species groups. In terms of anti-predatory benefits, the LMM (see Table 2.7) indicated that *Saimiri* vigilance was higher than *Sapajus*, but that overall vigilance was lower when in mixed-species groups. The findings on vertical stratification at Peperpot Nature Park were quite different, for instance *Saimiri* were observed more in higher forest strata when in single-species than when *Sapajus* were present (Figure 2.20 B), and *Sapajus* would forage less and be slightly more vigilant when *Saimiri* were also present. Possible reasons for these differences in behaviour and vertical stratification could be attributed to differences in forest composition (see de Almeida Rocha, De Vleeschower, Reis, Grelle & Oliveira, 2015). Observations of mixed-species groups occurred mostly in bamboo patches, which could also account for the lower proportion spent in higher level canopy. There were also fewer aerial predators present at Peperpot. However, despite the differences in habitat and vertical stratification the results of the models (see Tables 2.8 and 2.9) were very similar to the findings at Raleighvallen (see Table 2.10)

It would seem, that in addition to vertical segregation, difference in body size ratios and dietary overlap, the environment and seasonal variation are also important factors for the formation and maintenance of mixed-species groups. Zoological parks should therefore consider the benefits of field research for better understanding the natural history of their display animals in order to care for them adequately in the captive environment (Hediger, 1950; Kleiman, 1989; Buchanan-Smith & Hardie, 1997; Kerridge, 2005; Zimbler-DeLorenzo & Stone, 2011). In the case of the two mixed-species exhibits of *Sapajus* and *Saimiri* at Living Links, *Saimiri* would for instance require substrates that resemble the forest understory in order to have the cover needed to locomote between locations within the outdoor enclosure (i.e. protection from potential aerial predators, see Zimbler-DeLorenzo & Stone, 2011). Furthermore, large vertical and horizontal structures would be useful for *Sapajus* in order to encourage more natural locomotion and provide opportunities for lower ranking individuals to escape from those that are more dominant (or those that are receivers of aggression). Moreover, if we want to encourage *Sapajus* and *Saimiri* to interact then there would need to be some overlap in these structures to allow efficient space use by both species (see Chapter 3 for more details).

It was not possible to distinguish between different groups or individuals, and it was not always possible to continue follows for long durations, limiting the quantification of the nature of associations. Yet despite these limitations the findings from Raleighvallen and Peperpot provide some support for the advantages of mixed-species grouping; reduced vigilance (see Table 2.10), and that the two species were co-present and overlapping in time and space use (i.e. prerequisite 3 – see Section 1.1; Figure 1.1). In addition to this, it appeared that *Saimiri* were actively seeking *Sapajus* in both locations (i.e. social attraction), which is in keeping with previous research (Fleagle et al., 1981; Terborgh, 1983; Podolsky, 1990; Pinheiro et al., 2011; Frechette et al., 2014), as mixed-species observations occurred from either following a troop of *Saimiri* and coming across a troop of *Sapajus* or whilst observing *Sapajus* a troop of *Saimiri* approached. But due to the small samples obtained and the rarity of observing mixed-species groups during the study, neither of the study sites provided definitive data that could be used to make inferences about group stability (i.e. prerequisite 1 – see Section 1.1).

It was extremely useful for me to observe my study species in two different types of wild setting (primary and secondary forests), however it is clear that in order to test the groupness of mixed-species groups more robustly, a long-term field study would be required where different groups and individuals can be identified. Additionally, the methods for quantifying groupness need to be tested and refined. A promising way this could be achieved is by using a combined field-captive approach to the research of mixed-species groups, where methods can be tested in the field, and then brought back and refined and re-tested in captivity. In the interim, as it is already possible to study individuals in captivity living within a mixed-species exhibit, I am better able to examine what effect the presence of a congener has on both the behaviour and use of space. Though it must be acknowledged that compared to the wild, captive environments provide a limited amount of space, social restrictions (e.g. inability of individuals to emigrate), lack of predation as a real threat and regular supplies of food. But despite these factors, captive research is still useful in its contributions towards gaining a better understanding of how groups behave and interact with their environment(s). Chapter 3 provides the general methodology for studies conducted at Living Links including study site description for the remaining data Chapters of this thesis which investigate mixed-species enclosure use (Chapter 4), behavioural synchrony (Chapter 5) and social network analysis (Chapter 6) as methods for quantifying 'groupness' (see also Figure 1.1).

3 CAPTIVE DATA COLLECTION: GENERAL METHODOLOGY & STUDY SITE

3.1 Introduction

The following chapter provides the general methodologies for the research undertaken at the Living Links to Human Evolution Research Centre, Royal Zoological Society Scotland's Edinburgh Zoo (hereafter Living Links). More specifically, chapters discuss the differences in the use of three-dimensional space by *Sapajus* and *Saimiri* in their indoor and outdoor enclosures (Chapter 4), mixed-species behavioural synchrony between *Sapajus* and *Saimiri* (Chapter 5) and mixed-species social networks between *Sapajus* and *Saimiri* (Chapter 6). All of these studies were carried out with the same four groups of monkeys (n.b. newborns from the West *Saimiri* group were not included in the study and no deaths or transfers occurred during the study period). More detailed methods and procedures of the individual studies discussed are outlined in the relevant chapters.

3.2 Study Site

3.2.1 Location

Living Links was opened in 2008. It is a mixed-species exhibit housing two groups of tufted brown capuchins (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) in mirrored indoor and outdoor enclosures (Figure 3.1). Since its opening there have been four broad research themes: (1) social learning and cultural transmission; (2) communication and language; (3) understanding the world; and (4) welfare and mixed-species living. The fourth theme is now better known as the 'Living Together' project. While Living Links is primarily a research facility it also acts as a public engagement with science centre, the first of its kind within the United Kingdom, and the second in Europe (for more details regarding public engagement activities at Living Links see Bowler, Buchanan-Smith & Whiten, 2012; MacDonald & Whiten, 2011).

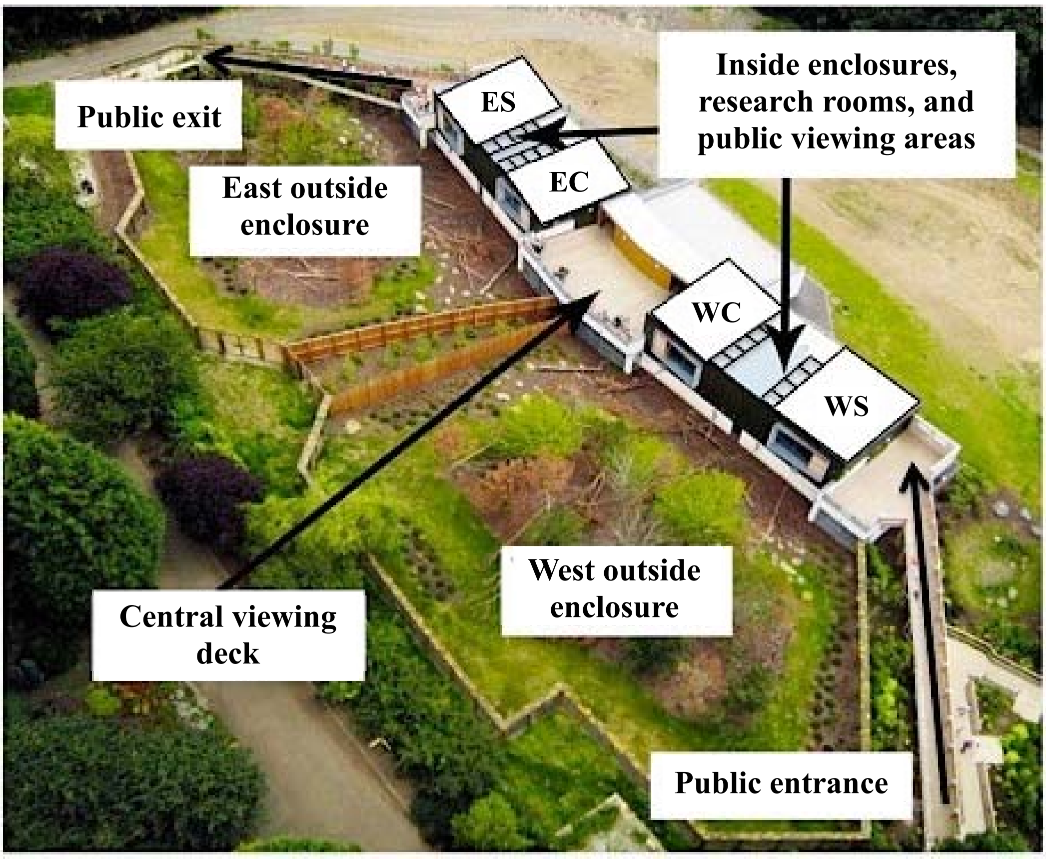


Figure 3.1 The Living Links to Human Evolution Research Centre. The shared outside enclosures are shown for the East and West groups, along with the monkeys' indoor enclosures (WS and WC = West squirrel monkeys and West capuchins; ES and EC = East squirrel monkeys and East capuchins) and research rooms, and the indoor and outdoor public viewing areas.

3.2.2 Housing & Husbandry

Living Links was specifically designed to accommodate both species of monkey and provides spacious naturalistic enclosures to allow the monkeys to exhibit species typical behaviours, promoting high welfare (see FAWC, 1979, 1992; Mellor & Reid, 1994; Mellor, 2016). Both the East and West exhibits (Figure 3.1) include an indoor enclosure for *Sapajus* (7 m x 4.5 m x 6 m high), an indoor enclosure for *Saimiri* (5.5m x 4.5m x 6m high), to which there is a size restriction on the entrance/exit, whereby only *Saimiri* can enter. Holding cages are connected to the indoor enclosures and are out of view to the public. The *Sapajus* holding cage measures 239cm x 150cm x 214cm and 275cm x 213cm x 214cm for *Saimiri*. These are used regularly by the RZSS keepers to perform routine animal husbandry and general check-ups on the monkeys. The monkeys also have a shared outdoor enclosure of approximately 900m^2 (see Leonardi et al., 2010, for more details), with the East and West groups being physically separated by a double fence line (Figure 3.1). Despite this the East and West groups (mostly *Sapajus*) are still able to communicate vocally and visually (e.g. when high up in the trees). Indoor temperatures are approximately 24°C, maintained using radiant ceiling heaters and the air conditioning system, and outdoor temperatures ranged between 12ºC and 25ºC during the study period (May-August 2015).

Both species had three different ways in which to access their outdoor enclosures: 1) via a doorway directly connected to their indoor enclosures, 2) through the off-show area (‘holding cages’), which is connected to their indoor and outdoor enclosures via a mesh tunnel, 3) through a series of two tiers of ‘cubicles’ in the research rooms which also connects both indoor and outdoor enclosures (Figure 3.1). In general, the monkeys had near-permanent access to one or more of these areas, however on occasions areas could be restricted when enclosures needed to be cleaned, or during certain experimental set ups.

A team of seven keepers are responsible for the daily care and husbandry of the monkeys, ensuring a high standard of welfare. Daily routines were similar to previous observation periods as detailed by Leonardi, Buchanan-Smith, Dufour, MacDonald and Whiten (2010) and Buchanan-Smith, Griciute, Daoudi, Leonardi and Whiten (2013). The main feeds would take place in the morning and afternoon (in the indoor enclosures), consisting of pre-measured commercial TrioMunch pellets, supplementary vitamins and minerals and specially formulated Marmoset Jelly along with a mixture of fresh fruits and vegetables (food was placed onto various feeding platforms rather than just clumped in one place).

Saimiri were also given Milupa (similar to porridge) and insects every day and *Sapajus* would be given a scatter feed of apples at lunchtime, usually in the outdoor enclosure before/during the scheduled educational talk to the public (n.b. *Saimiri* were not usually separated for this unless required for the purpose of research). Additionally, both species received chicken, potatoes and boiled eggs at least once a week, with water available *ad libitum*. The keepers also provide environmental enrichment each month (e.g. puzzle feeders, paddling pools see Figure 3.2) when there is no experimental testing occurring in the research cubicles.

Figure 3.2 Enrichment (razor clams in paddling pools) provided by Living Links keepers in the East (A) and West (B) outdoor enclosures.

3.3 Study Subjects

Living Links houses two populations of Guianan brown capuchins (*Sapajus apella*) and Guianan squirrel monkeys (*Saimiri sciureus*). There were 17 individuals of both *Sapajus* and *Saimiri* in the East exhibit, 18 individuals in the West *Sapajus* and 9 in the West *Saimiri* group (see Table 3.1). Since opening in 2008 the number of individuals has changed due to births, deaths and transfers with only the West *Saimiri* remaining as a breeding group at the time of the study; this was due to the introduction of a new alpha male (risk of in-breeding in other groups).

Table 3.1 *Study subjects: East* Sapajus *(n=17),* East Saimiri *(n=17), West Sapajus (n=18), West Saimiri (n=9).*

Name	**Genus**	**Sex**	**Age range (in years) during study**	**Exhibit**	**# of observations (In/Out)**
Popeye	*Sapajus*	M	13-14	East	11/79
Anita	*Sapajus*	F	17	East	17/70
Junon	*Sapajus*	F	14-15	East	7/83
Kato	*Sapajus*	M	9-10	East	20/70
Manuel	*Sapajus*	M	11	East	16/72
Penelope	*Sapajus*	F	9	East	14/72
Carlos	*Sapajus*	M	8-9	East	28/59
Chico	*Sapajus*	M	6	East	38/47
Rosa	*Sapajus*	F	5	East	18/67
Reuben	*Sapajus*	M	4-5	East	21/63
Sol	*Sapajus*	F	4-5	East	20/62
Flojo	*Sapajus*	M	3-4	East	16/72
Lindo	*Sapajus*	F	3-4	East	13/63
Willow	*Sapajus*	F	2	East	12/74
Nena	*Sapajus*	F	2	East	13/71
Gustavo	*Sapajus*	M	1	East	12/76
Agnes	*Sapajus*	F	1	East	11/77
Boa	*Saimiri*	M	9	East	23/37
Tatu	*Saimiri*	F	14	East	47/24
Roca	*Saimiri*	F	12	East	38/16
Maya	*Saimiri*	F	11	East	71/5
Elie	*Saimiri*	F	9	East	57/16
Cali	*Saimiri*	F	9	East	48/18
Pica	*Saimiri*	F	7	East	82/1
Yendi	*Saimiri*	F	6	East	29/34
Flora	*Saimiri*	F	6	East	40/19
Sipi	*Saimiri*	F	5	East	33/24
Lexi	*Saimiri*	F	4	East	32/28

Table 3.1. *continued.*

Dora	*Saimiri*	F	4	East	45/17
Amarilla	*Saimiri*	F	3	East	37/32
Pelusa	*Saimiri*	F	3	East	32/29
Gabriela	*Saimiri*	F	3	East	53/9
Valencia	*Saimiri*	F	3	East	42/25
Ciara	*Saimiri*	F	3	East	40/26
Diego	*Sapajus*	M	12-13	West	52/38
Lana	*Sapajus*	F	19	West	43/44
Santiago	*Sapajus*	F	13	West	45/44
Sylvania	*Sapajus*	F	11-12	West	38/47
Toka	*Sapajus*	M	10	West	46/43
Figo	*Sapajus*	M	9	West	33/52
Pedra	*Sapajus*	F	7	West	47/42
Mekoe	*Sapajus*	M	7	West	58/27
Inti	*Sapajus*	M	5	West	28/54
Rufo	*Sapajus*	M	5	West	29/56
Ximo	*Sapajus*	M	5	West	42/44
Torres	*Sapajus*	M	4	West	38/43
Luna	*Sapajus*	F	4	West	48/37
Alba	*Sapajus*	F	3	West	51/39
Mr Fudge	*Sapajus*	M	1-2	West	47/43
Bear	*Sapajus*	M	1-2	West	50/39
Hazel	*Sapajus*	F	1	West	47/39
Pixie	*Sapajus*	F	1	West	45/41
Hugo	*Saimiri*	M	4-5	West	47/20
Gerda	*Saimiri*	F	15	West	87/0
Jasmin	*Saimiri*	F	12	West	83/3
Toomi	*Saimiri*	F	8	West	73/14
Dita	*Saimiri*	F	5	West	75/9
Sancha	*Saimiri*	F	5	West	80/5
Orla	*Saimiri*	F	3	West	77/4
Gisele	*Saimiri*	F	2-3	West	79/4
Loki	*Saimiri*	F	1	West	64/22

Identifying age-sex classifications in animals is usually based on their behavioural and physical attributes, however the age at which they reach maturity is difficult to determine without taking biological samples. Though in some instances, behavioural characteristics can at least be used as a reliable proxy for sexual maturity. In general, modern zoos maintain detailed reports on animal copulations, birth records and previous rearing histories, making age-sex classifications much easier to establish than in wild populations. With this in mind, individuals were categorized (see Table 3.2 for descriptions) as follows: juveniles ≤3 subadults between 3-4 years in *Sapajus* and 2-3 years in *Saimiri*, and individuals above these ages were categorized as adults (DuMond, 1968; Izawa, 1980; Baldwin & Baldwin, 1981; Fragaszy et al., 2004).

Table 3.2 *Descriptions of age-sex classes for tufted capuchins (*Sapajus *spp.) and squirrel monkeys (*Saimiri *spp.) based on physical traits and following DuMond (1968), Baldwin and Baldwin (1981), Izawa (1980) and Fragaszy et al. (2004).*

Age-sex classification	***Sapajus***	***Saimiri***
Adult male	≥ 4 years Broad (square shaped) face with pronounced jaw, broad shoulders and generally larger build than adult females.	≥ 3 years Broad jaw (generally larger rounded head), larger torso, shoulders and arms (fatted male**).
Adult female	≥ 4 years (reached sexual maturity*) Prominent tufted hair on either side of crown, and generally more slender than adult males.	≥ 3 years (reached sexual maturity*) Similar size to adult males, though more slender in shape. Dark (black) dots or lines at either side of face (sideburns).
Subadult	3-4 years Males and females are of a similar size and difficult to distinguish. Still spend some time playing, and males may be found on the periphery of the group.	2-3 years Smaller than adults, males and females are of a similar size and difficult to distinguish. Still spend some time playing.
Juvenile	1-3 years Smaller than subadults, independent but still spend a lot of time with their mother, and may occasionally nurse. Play makes up large proportion of daily activities.	1-2 years Smaller than subadults independent but still spend a lot of time with their mother, and may occasionally nurse. Play makes up large proportion of daily activities.
Infant	≤ 1 year New-born to very young, extremely dependent on mother (mostly clinging to mother's back).	≤ 1 year New-born to very young, extremely dependent on mother (mostly clinging to mother's back). From 6 months becomes increasingly independent of mother.

*Females are sexually mature once they have started an oestrous cycle.

**Adult 'fatted' male *Saimiri* will put on 70% of their own body weight in water retention during the breeding season (DuMond, 1968).

The *Sapajus* were distinctive enough to be identified individually, whereas identifying the *Saimiri* required artificial aids (chain collars with colour coded beads), though these often fell off and so identification without these was also necessary. The date of birth, parentage, and source location of all but one of the monkeys at Living Links was known. One adult male from the East *Sapajus* group (Kato), was born in the wild and hand-reared by humans, whereas all others were born in captivity and mother-reared (Dufour, Sueur, Whiten & Buchanan-Smith, 2011). All of the Living Links capuchins are pure breeds (*Sapajus apella*) and are part of the 'European Brown Capuchin Stud Book' (Roberts & Quintard, 2009) and the West group of squirrel monkeys are also pure breeds (*Saimiri sciureus*) part of the 'European Common Squirrel Monkey Stud Book' (Vermeer, 2006). However, the East squirrel monkeys are hybrids, and as a result it is only possible to document the parentage of those for which the information has been made available (see Appendix III for information relating to pedigrees of *Sapajus* and *Saimiri* groups.)

3.4 Data Collection

The data were collected by direct observation during the opening hours of the zoo (09.00-17.00) throughout the week. Experimental sessions in the research rooms were generally scheduled on Mondays, Tuesdays, Thursdays and Fridays (11.15-12.45 and 14.15-15.45), due to these sessions excluding individuals from the group, data were only collected outside of these times.

Both scan and focal sampling (Altmann, 1974a; Martin & Bateson, 2007) were used to obtain proximity, interaction and behavioural data for *Sapajus* and *Saimiri* in their indoor and outdoor enclosures. All observations were made via the public viewing platforms (Figure 3.1) and recorded directly onto data sheets (Appendix IV). However, before data collection could even begin, it was essential for me the principal investigator (PI) and my research assistant (RA) to first be able to identify each individual monkey, which was achieved by help from the keepers, photographic IDs and the Living Links Research Coordinator (L. Wood). More detailed methodologies are outlined in each data chapter (4, 5, and 6). The RA was trained by the PI for data collection requiring the use of scans, descriptions of behaviours (see Table 3.3) and weather (see Table 3.4) were provided, and inter-observer reliability was tested during pilot data collection (see Martin & Bateson, 2007); reliability needed to be ≥80% before real data collection could begin.

Table 3.3 *Definitions of behaviours used to examine the effect of individual activity budgets on behavioural synchrony in the monkeys at Living Links (taken and adapted from Leonardi et al., 2010).*

Behaviour	Definition
Locomotion	Monkey is moving in relation to its surroundings from one point to another, either at a rapid pace (i.e. running speed and also includes jumping and leaping when there is more than one leap/jump made) or at a slow pace (i.e. walking speed, can also include single leap/jump).*
Vigilant/Alert	Monkey is stationary and appears to be visually attentive i.e. visual scans of surroundings or watching other monkeys / people. Head and body are erect/tense.
Rest/Sleep	Monkey is stationary and not engaged in any of the activities/behaviours described. Monkey appears to be visually inattentive (eyes may be open or closed and may be asleep) and does not perform visual scans of the environment. Includes sleeping.
Play	Monkey engages in high activity interaction (e.g. chase, rough and tumble, mock wrestling) with other individuals. This can include non-aggressive physical contact, or distance play, e.g. hopping and running, steep leaps (almost vertical jumps with minimal forward locomotion) or swinging by the feet, while visually checking/coordinating with play partners. Behaviours which are used to elicit play are also included, e.g. looking through legs or playfully rolling/lolling on back while looking at potential play partner.
Forage/Eat	Monkey is actively searching its environment for food items. Includes manipulating food with hands or feet, or holding food, e.g., while inspecting food item. Monkey is eating a food item, including holding and nibbling, chewing inside the mouth. *Examples: Monkey is engaged in foraging as described above, to obtain fruit, vegetables, seeds, nuts, edible plants and other edible items which may be provided by the keepers.* *Monkey is engaged in foraging as described above, to obtain insects. Includes stalking behaviours, visually tracking insect movements (which at times involves freezing position) and grabbing at insects. Includes those provided by the keepers (which are given alive, e.g. locusts and crickets etc) and also includes live feed such as meal worms.*
Groom	The monkey's hands and/or lips are drawn through the coat, skin or teeth of another individual and particles are occasionally removed. Also includes being groomed by another monkey.*

Table 3.3 *continued.*

Aggression/Conflict	Monkey is involved in an aggressive conflict with one or more other monkeys of either species, either as the aggressor or in defence. This can include facial threats (e.g. retracted lips, with mouth open in capuchin monkeys), grimaces and/or vocalisations (e.g. shrieks or screams), intense rapid movements towards another individual which lead to displacement, chasing (contact and no contact) where one or more monkeys actively pursues one or more monkeys, vigorous shaking of branches and vines or aggressive physical contact such as grasping, slapping, pulling, biting or jumping onto.*
Solitary	No monkey within two body lengths away from the focal.

* adapted from Leonardi et al. (2010) combined fast and slow locomote into one category and combined intra- and inter-specific aggression into one category.

Table 3.4 *Definitions of weather conditions.*

Weather conditions	**Definitions**
Clear	Sunny and the sky is virtually free of clouds.
Light clouds	Clouds are white and cover less than 60% of the sky.
Cloudy	Clouds are white and cover more than 60% of the sky.
Overcast	Clouds are 'thick' and grey in colour, covering more than 90% of the sky.
Rain*	Precipitation including light drizzle, to heavy downpours.
Windy*	Air flow is brisk or blustery, does not include light breeze.

**Note in conjunction with other weather*

3.5 Data Analysis

Transcribed data were analysed using Microsoft Excel 2016, IBM SPSS version 23, R (version 3.6.3) in the RStudio environment (R Core Team, 2020; RStudio, 2020) and SOCPROG version 2.9 (Whitehead, 2009). Details of the specific statistical tests applied are provided in the relevant chapters. All data were tested for normality (e.g. Kolmogrov-Smirnov test, Shapiro-Wilk test or Levene's test) and if normality assumptions were not met then non-parametric tests were applied.

3.5.1 Scan sampling

The modified Spread of Participation Index (SPI) (Plowman, 2003) was applied in order to determine *Sapajus* and *Saimiri*'s use of space within enclosures (see Chapter 4). This method was chosen because it allows for the use of unequal zones, thereby allowing for more meaningful areas of enclosures to be monitored. The SPI was calculated in Microsoft Excel 2016 and all other analyses were conducted using IBM SPSS version 23: Mann-Whitney *U* tests were used to test the significance between observed data for zones and heights with expected values, and the Wilcoxon's test was applied to SPI data for 3-D indoor and outdoor enclosure use (Field, 2009). Linear regressions were used to determine whether age could explain variation in enclosure use based on SPI values.

The degree of behavioural synchrony between *Sapajus* and *Saimiri* was calculated using Simpson's Diversity Index in Microsoft Excel 2016 (see Chapter 5). All analyses were conducted using R (version 3.6.3) in the RStudio environment (R Core Team, 2020; RStudio, 2020): Mann-Whitney *U* tests were used to compare observed and randomly generated synchrony scores to assess whether they differed from what would be expected by a simple model (i.e. monkeys behaving independently of each other). Levene's test was applied to assess whether the variation found in both observed and randomly generated samples differed from what would be expected by chance, and linear models (LMs) and linear mixed models (LMMs) were used to examine what variables contribute to behavioural synchrony.

3.5.2 Focal sampling

When documenting interactions or proximity data between individuals, focal sampling was used (Martin & Bateson, 2007) and social network analyses (SNA) were then applied using SOCPROG 2.9 (Whitehead, 2009) to generate association indices (see Chapter 6). SNA is the study of social groups as networks of nodes connected by social ties, and enables us to both identify and quantify specific attributes of social relationships within populations of known individuals (Croft, James & Krause, 2008; Krause, Lusseau & James, 2009). It is now a widely applied method of analyses in behavioural ecology but despite its clear potential, it has seen little use in the application to animal management in zoos (Rose & Croft, 2015). Whilst some research has already been conducted on social networks in captive single-species groups of *Sapajus* (see Dufour et al., 2011; Morton, 2014) and *Saimiri* (see Dufour et al., 2011; Claidière, Messer, Hoppitt & Whiten, 2013) at Living Links, no research has yet looked at mixed-species social networks.

3.6 Public Engagement

Making science accessible to non-academics has become increasingly important within the scientific community, but it is often difficult to achieve. Zoos can provide an ideal platform for public engagement and science communication given the number of visitors attracted to them. For instance, the RZSS Edinburgh Zoo (hereafter zoo) attracts approx. 672,000 visitors annually and has an online community of over 120,000 Facebook and Twitter followers. Living Links enables the many people who visit the zoo to observe and interact with ‘live’ science (when studies are underway) as well as engagement facilities (e.g. information boards on the monkeys and research being undertaken, videos and puzzles) present within the Centre (see Bowler et al., 2012; MacDonald and Whiten, 2011).

While collecting data, I would often come into contact with members of the public enquiring about the research taking place at Living Links. In addition to these informal and opportunistic discussions with the public, I also participated in scheduled presentations, where Living Links researchers, education officers and keepers would talk to the public regarding the different studies taking place and the management of the animals living there. In addition to this I have presented my research in the Budongo Trail Lecture Theatre, RZSS Edinburgh Zoo to zoo staff and members of the board, other Living Links and Budongo Trail researchers, and zoo visitors (including those that have zoo membership). These forms of public engagement provide a useful way to communicate the research being undertaken, the procedures and practices in place to maintain the health and wellbeing of its animals, and the contributions towards conservation efforts.

3.7 Ethical Statement

The research conducted for this thesis was non-invasive and abided by the Association for the Study of Animal Behaviour Ethical Guidelines (ASAB, 2012) and the British Psychological Society’s guidelines for psychologists working with animals (BPS, 2012). The research was also approved by the Psychology Ethics Committee at the University of Stirling, Scotland and the Living Links Management Board (see Appendix V).

4 3D ENCLOSURE USE IN A MIXED-SPECIES EXHIBIT

The following chapter is adapted from work that was published in the journal Animal Behavior and Cognition (Daoudi, Badihi & Buchanan-Smith, 2017). For the original manuscript see: https://osf.io/gres4/

4.1 Abstract

One of the key features of living in a group, is being co-present in time and space. *Sapajus* and *Saimiri* are known to form mixed-species groups in the wild, though they are generally observed in different levels of the canopy (i.e. *Saimiri* in the understory and *Sapajus* in mid to upper levels - see Chapter 1, Section 1.7). In captivity the physical environment is often less varied than the wild and does not always offer opportunities for animals to engage in natural behaviours, such as jumping and leaping between vertical structures for arboreal primate species. Therefore, the physical features of the captive environment, including both the useable space and environmental complexity, can have a significant influence on primate behaviour and ultimately animal welfare, especially when considering the needs of two different species in a shared exhibit. This study examined the patterns of proximity in time and space use by *Sapajus* and *Saimiri* in their indoor and outdoor enclosures, using the modified spread of participation index (SPI). I found that in the shared outdoor enclosures *Sapajus* showed a preference for central zones, while *Saimiri* appeared to prefer zones on

the periphery of their outdoor enclosures, close to doorways leading back to indoor enclosures. This separation of proximity in time and space use by the monkeys indicate that they are not behaving as a true mixed-species group, and there is not much evidence for social attraction.

4.2 Introduction

One of the prerequisites of living in a group identified in Chapter 1 (see Section 1.1), is that individuals should be co-present in time and space (e.g. Parrish & Hamner, 1997; Ward & Webster, 2016 - see also Figure 1.1). A captive environment will generally impose spatial limitations on its inhabitants when compared to their natural environments (Hediger, 1950; Kleiman, 1989; Buchanan-Smith & Hardie, 1997; Kerridge, 2005; Ross, Schapiro, Hau & Lukas, 2009 – see also Chapter 2, Section 2.2.1), which may be why the display of captive animals in naturalistic exhibits (with access to both indoor and outdoor enclosures) has become increasingly prevalent within modern zoos. The principal aims of a more naturalistic setting is to provide more complexity and choice within the captive environment and to promote the increase of positive (and more 'natural') species-specific behaviours, such as climbing and leaping in arboreal non-human primates (Stoinski, Hoff & Maple, 2000; Badihi, 2006). Additionally, such environments should prevent or decrease negative stereotypical behaviours (e.g. locomotor pacing) or anxiety-related self-directed behaviours such as self-scratching and self-grooming (Baker & Aureli, 1997; Buchanan-Smith, Prescott & Cross, 2004). By providing sufficient space, proper (species-appropriate) facilities and company of the animal's own kind, they are better able to 'express normal behaviour' (see FAWC, 1992; Mellor & Beausoleil, 2015; Mellor, 2016 – see also Chapter 2, Section 2.2.1) and as such provide study subjects that can be better compared to congeners in the wild. Evaluations of naturalistic exhibits show that they have been relatively successful in achieving this, with more 'normal behaviours' observed compared to animals housed in smaller and more barren/unstimulating environments (Clarke, Juno & Maple, 1982; Maple & Finlay, 1986; Reinhardt, Liss & Stevens, 1996; Buchanan-Smith et al., 2004; Hosey, 2005). Furthermore, animals housed in smaller indoor enclosures have been found to be less active than those housed in larger, outdoor enclosures (Macedonia, 1986).

There is an increasing awareness of the variations in the physiology, behaviour, ecology and locomotion of different primate species as a result of their adaptations to different environments (Buchanan-Smith et al., 2004; Hosey, 2005 – see also Chapter 2, Section 2.2.1). While there are clear benefits (in terms of the animals' biological and welfare requirements) to housing captive animals in larger and more naturalistic enclosures, they can be of limited value if the animals are unable to make use of all of the available space (e.g. due to lack of or inappropriate substrates – Paulk, Dienske, & Ribbens, 1977; Ogden, Finlay, & Maple, 1990; Kerl & Rothe, 1996; Buchanan-Smith et al., 2004; Estevez & Christman, 2006; Ross & Lukas, 2006; Ross et al., 2009). For instance, Stoinski et al. (2000) found that a captive group of Western lowland gorillas (*Gorilla gorilla gorilla*) spent 50% of their time in less than 15% of their enclosures and displayed a preference for areas near structures, such as their holding building. Similarly, a study on lion-tailed macaques (*Macaca silenus*) found that they spent 43% of their time in less than half of their enclosure space (Mallapur, Waran, & Sinha, 2005). Additionally, having access to vertical space has been found to be important for arboreal non-human primates in captivity, as they tend to occupy higher areas (>4 m) of their enclosures rather than being on the ground (Buchanan-Smith et al., 2004; Hebert & Bard, 2000; Leonardi et al., 2010; Poole, 1991; Ross, Calcutt, Schapiro, & Hau, 2011; Traylor-Holzer & Fritz, 1985). The age of individuals should also be considered. Juveniles, though smaller than adults, are usually found to be more active than adults and therefore may have greater space requirements for physical development and play (Traylor-Holzer & Fritz, 1985; Wells & Turnquist, 2001; Buchanan-Smith et al., 2004).

For the most part, studies on space use in captive animal groups have generally focussed on single-species groups (e.g. Macedonia, 1986; Ogden et al., 1990; Stoinski et al., 2000; Mallapur et al., 2005; Ross & Lukas, 2006; Ross et al., 2009; Ross et al., 2011), and while there are some studies that focus on enclosure use of animals housed in mixed-species exhibits (e.g. Dalton & Buchanan-Smith, 2005; Leonardi et al., 2010; Clark & Melfi, 2011), none has yet focussed on studying the patterns of proximity in time and space use (an aspect of prerequisite 3) as a quantitative measure of groupness in captive mixed-species groups. In this chapter I explore space use in two mixed-species groups of Guianan brown capuchin (*Sapajus apella*) and Guianan squirrel (*Saimiri sciureus*) monkeys, housed at Living Links, in order to determine if the species are overlapping in time and space (an aspect of prerequisite 3) and are attracted to (i.e. proximity is not due to aggregating around a resource), or avoid each other (i.e. two separate groups sharing an exhibit) and what this implies in relation to their welfare.

Of the Neotropical primate species known to form mixed-species groups, these two have the greatest relative difference in body size (*Sapajus* are larger than *Saimiri* see Chapter 1, Section 1.7), and due to these differences they tend to occupy different levels of the canopy, with *Sapajus* generally in the mid to lower levels of the main canopy, and *Saimiri* in the understory (Klein & Klein, 1973; Fleagle, Mittermeier, & Skopec, 1981; Terborgh, 1983; Podolsky, 1990; Boinski, 1999 – see also Chapters 1 and Chapter 2). As such it is expected that in captivity the monkeys will likely be separated vertically (i.e. *Sapajus* on substrates higher up than *Saimiri*). Furthermore, as has been noted extensively in Chapter 1, the two main forces driving grouping are foraging advantages and reduced risk of predation (see Sections 1.2 and 1.3), however in captivity there is no need to group for these reasons (e.g. food is provided and there is little to no risk of predation). Therefore, if animals are still choosing to group in captivity then this could be due to social attraction (i.e. individuals seek out the presence of others in the group – see Latané, Schneider, Waring & Zweigenhaft, 1971; Strayer, Bovenkerk & Koopman, 1975; Schino, 2001; Tiddi, Aureli & Schino, 2010; Ward & Webster, 2016). Previous studies at Living Links have found that individuals of both species spent ~80% of their time in shared enclosures (both indoor and outdoor), and that both *Saimiri* groups were observed frequently in the *Sapajus* indoor enclosures (Leonardi et al., 2010; Buchanan-Smith et al., 2013), which indicates an element of social attraction.

The aims of the study are as follows:

(1) To examine the differences in three-dimensional space use by *Sapajus* and *Saimiri* in their different enclosures (e.g. height and location/zone). It is expected that *Sapajus* will generally be in higher levels compared to *Saimiri*, and if they are behaving as a true mixed-species group, then it is expected that they will still occupy the same areas;

(2) To assess whether the two species are behaving as a true mixed species group by being co-present in an enclosure and overlapping in time and space (due to social attraction). If *Sapajus* and *Saimiri* are behaving as a true mixed-species group, then it is expected that they will be observed in overlapping zones (but may be at different heights – *Saimiri* lower down than *Sapajus*). However, if they are behaving as two

single-species groups that live in a shared exhibit then it is expected that they will be observed in different areas of the enclosure;

(3) To assess whether there is a difference in space use according to the age of individuals, for instance younger individuals (of both species) might be expected to use more of the available space (and as such mix more) compared to adults.

4.3 Methods

4.3.1 Subjects

Two mixed-species groups of *Sapajus* and *Saimiri* housed at Living Links were included in the study. There were 17 individuals of both *Sapajus* and *Saimiri* in the East exhibit, and in the West exhibit there18 *Sapajus* and 9 *Saimiri* (see Table 4.1). Individuals were categorized as subadults at ≤4 years in *Sapajus* and ≤3 years in *Saimiri*, and individuals above these ages were categorized as adults. For more specific details on subjects and housing and husbandry please refer to chapter 3 (Section 3.2.2).

4.3.2 Design & Procedure

Data were collected during June-August 2015 by G. Badihi (see Chapter 3, Section 3.4 for details on inter-observer reliability). Scan sampling methods (Martin & Bateson, 2007) were used to record the location (*Sapajus/Saimiri* indoor or outdoor), zone and height occupied for each individual, sampling both species in the mixed exhibits. Scans were collected for all group members within 20 minute intervals for either West or East groups. We first recorded each individual in the indoor enclosure (*Sapajus* followed by *Saimiri*), choosing individuals from left to right, then individuals in the outdoor enclosure, and finally collected data on any individuals who had not been recorded. If an individual was not observed during a scan, then that individual would be recorded as out-of-sight. Each enclosure was divided and coded into meaningful zones (see Figures 4.1 – 4.2 and Table 4.1) and heights occupied were categorized as ground level, <2 m, 2–4 m and >4 m, following Leonardi et al. (2010). Recording took place between 09.00 and 17.00 hr, with a similar number of scans divided into three time frames: morning (09.00-12.00), midday (12.00-14.00) and afternoon (14.00-17.00). We accumulated a total of 180 scans divided equally between West and East.

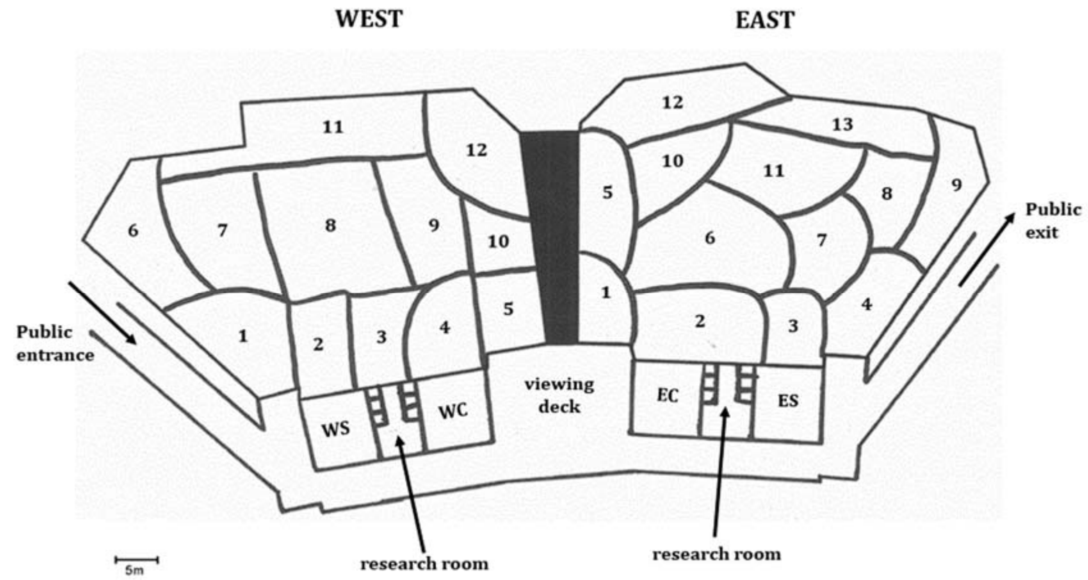


Figure 4.1 Schematic diagram of the Living Links outdoor enclosures, divided into 'meaningful zones' (approximately to scale), for example zone 2 East represents woodchip and tree logs on the ground and zone 3 West represents tall grass and wildflowers (see Table 4.1 for more details of zones). **Key for indoor enclosures: WS and WC = West *Saimiri* and West *Sapajus*; ES and EC = East *Saimiri* and East *Sapajus*.**

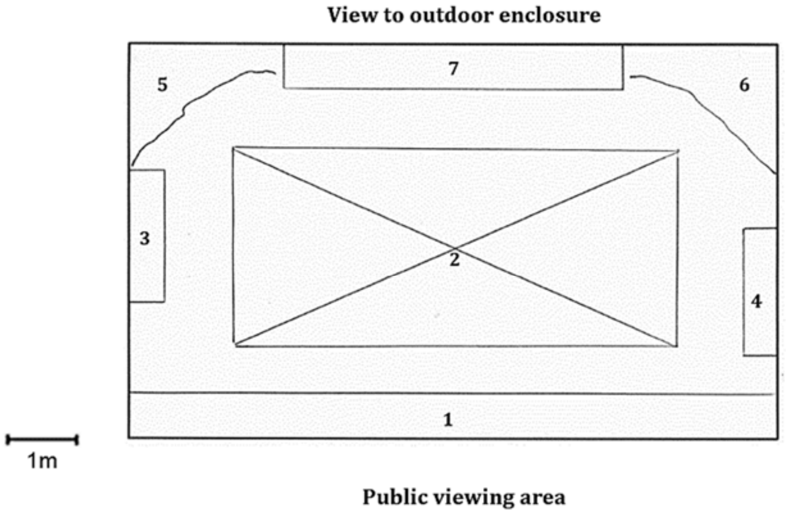


Figure 4.2 Schematic diagram of the Living Links, indoor enclosure, divided into meaningful zones (approximately to scale): (1) large window and window sill where the visitors can see into the indoor enclosure; (2) the central tree log platforms and scaffolding, in a rectangular shape with criss-crossing sections (on two levels), and surrounding blank areas; (3) small upper window and window sill (on the right of the West *Saimiri* and East *Sapajus* and on the left of the West *Sapajus* and East *Saimiri*); (4) large lower window and window sill – can see into the cubicle research area (on the left of the West *Saimiri* and East *Sapajus* and on the right of the West *Sapajus* and East *Saimiri*); (5) Rock wall and rock ledge to the back left of the enclosure; (6) rock wall and rock ledge to the back right of the enclosure; (7) large window and window sill at the back of the enclosure.

Table 4.1 *Descriptions of the 'meaningful zones' within the West and East outdoor enclosures.*

Zone	**West**	**East**
1	Large rocks protruding from the ground	Large rocks protruding from the ground and long tree logs
2	Large rocks protruding from the ground and long tree logs	Woodchip on ground and tree logs
3	Tall grass and wildflowers	Woodchip on ground and vines leading to small tree
4	Woodchip on ground, tree log and grass	Shrubbery and evergreen bushes
5	Large rocks protruding from the ground and long tree logs	Evergreen bushes running parallel to the fence line
6	Evergreen bushes	Small tree (looks like a Y shape), cluster of tall trees and short grass
7	Tree stump and tall trees in the shape of an H with a slanted/diagonal middle section (tree log) and bamboo	Group of 4 trees
8	Cluster of central tall trees, with resting platforms	Small pine trees and tall grass
9	Smaller trees and grass section	Evergreen bushes and tall grass
10	Large rocks protruding from the ground	Forked tree and flat platforms
11	Shrubbery, bushes and tall grass	Trees towards the back of the enclosure with wavy branches between trees
12	Tall grass and tree log	Tall grass and shrubbery
13	–	Tall grass

4.3.3 Data analysis

In order to determine how selectively *Sapajus* and *Saimiri* used their enclosure space, I used the modified spread of participation index (SPI) (Plowman, 2003) applying the following formula:

$$\text{SPI} = \frac{\sum |f_o - f_e|}{2(N - f_{e\,min})}$$

where f_o is the frequency of observations in a zone or height level, f_e the expected frequency of observations in a zone or height level, based on zone size or height assuming even use of the whole enclosure, $|f_o - f_e|$ is the absolute value of the difference between f_o and f_e, which is summed for all zones or height levels Σ, N the total number of observations and $f_{e\ \text{min}}$ the expected frequency of observations in the smallest zone or height.

The modified formula was used over the original formula by Dickens (1995), because it allows for unequal zones (Plowman, 2003). The index varies between 0 and 1, with 0 suggesting maximum enclosure use (i.e. all zones and heights occupied equally) and a value of 1 suggesting minimum use of enclosure (i.e. only one zone or height occupied).

Mann-Whitney *U* tests were used to determine whether the observed data for zones and heights occupied were consistent with the values expected under the fitted model (Field, 2009). Linear regressions were used to determine whether age can explain variation in enclosure use based on SPI values, and Wilcoxon's test was applied to SPI data for 3-D indoor and outdoor enclosure use.

4.4 Results

4.4.1 Enclosure use

Percentages of each species occupying each enclosure (indoor/outdoor) were calculated. Had support been found for social attraction, then there would have been a high percentage of both species occupying the same enclosures (i.e. be in proximity in time and space). However, this was only observed in the East group where *Sapajus* and *Saimiri* were co-present for 84% of scans, whereas in the West group the monkeys were only co-present for 34% of scans (see Table 4.2).

Table 4.2 *The percentage of scans (n = 90) that* Sapajus *and* Saimiri *were observed in their indoor and outdoor enclosures, out of sight, and co-present for both East and West Groups.*

Exhibit	**Species**	**% indoor enclosure(s)**	**% outdoor enclosure**	**% out of sight**	**% co-present**
East	*Sapajus*	16	80	4	84
	Saimiri	57	27	16	
West	*Sapajus*	47	49	4	34
	Saimiri	88	11	1	

Both *Sapajus* groups showed a preference for the central (tall tree) areas of their outdoor enclosures, with the East group observed in zone 6 for 48% of scans (Figure 4A) and the West group in zone 8 for 36% of scans (Figure 4C). Although both *Sapajus* groups appear to make use of most of their outdoor enclosure space, peripheral zones were used less than expected. For the East group, zone 1 which included substrates such as large rocks and long tree logs was significantly underused ($U = 57$, $z = -3.029$, $p = 0.002$, $r = -0.73$), as well as woodchip areas, zone 2 ($U = 86$, z = -2.017, $p = 0.044$, $r = -0.49$) and zone 3 ($U = 38$, $z = -3.677$, $p < 0.0001$, $r = -0.89$) in addition to areas with shrubbery and evergreen bushes, zone 5 ($U = 41.5$, $z = -3.605$, $p < 0.0001$, $r = -0.87$). Similarly, for West *Sapajus* areas including large rocks and long tree logs, zone 1 ($U = 60$, $z = -3.277$, $p = 0.001$, $r = -0.77$), zone 2 ($U = 17$, $z = -4.607$, $p < 0.0001$, $r = -1.09$) and zone 5 ($U = 64.5$, $z = -3.121$, $p = 0.002$, $r = -0.74$) and areas with shrubbery, evergreen bushes and tall grass, zone 6 ($U = 36$, $z = -4.205$, $p < 0.0001$, $r = -0.99$) were significantly underutilised.

By contrast both *Saimiri* groups showed a preference for peripheral areas of their outdoor enclosure with a high percentage of scans being in proximity to their indoor enclosure entrances. The East group were observed in zones 2 and 3 for 24% and 34% of scans respectively (Figure 4B) and the West group in zone 2 for 60% of scans (Figure 4D). For both *Saimiri* groups the central tree areas were utilised significantly less than expected; East, zone 6 ($U = 28$, $z = -4.022$, $p < 0.001$, $r = -0.98$) and zone 7 ($U = 46$, $z = -3.427$, $p = 0.001$, $r = -0.83$); West, zone 7 ($U = 13.5$, $z = -2.498$, $p = 0.013$, $r =-0.83$), zone 8 ($U = 10.5$, $z = -2.705$, $p = 0.01$, $r = -0.90$) and zone 9 ($U = 11.5$, $z = -2.683$, $p = 0.01$, $r = -0.89$). Other areas that were significantly underused by East *Saimiri* were zones including trees, such as zone 8 ($U = 17$, $z = -4.64$, $p < 0.001$, r = -1.13), zone 10 ($U = 15.5$, $z = -4.695$, $p < 0.0001$, $r = -1.14$) and zone 11 ($U = 17$, z = -4.64, $p < 0.001$, $r = -1.13$) and areas with tall grass, zone 13 ($U = 17$, $z = -4.64$, $p < 0.001$, r = -1.13). The West *Saimiri* were also observed significantly less than expected in zones that were towards the back of the outdoor enclosure, zone 6 ($U = 4.5$, $z = -3.514$, $p < 0.001$, $r = -1.17$), zone 9 ($U = 11.5$, $z = -2.683$, $p = 0.01$, $r = -0.89$) and zones 10, 11 and 12 ($U = 4.5$, $z = -3.492$, $p <0.001$, $r = -1.16$).

For indoor enclosure use, both the East and West *Sapajus* groups and West *Saimiri* group were observed for a high proportion of scans in zone 2 (the central rectangular, with criss-crossing mid sections, log platforms and scaffolding), 70%, 68%, and 72% respectively (Figure 4A, C, D). While the East *Saimiri* were observed using zone 7 (the large window and windowsill at the back of the enclosure) for 40% of scans (Figure 4B). In the East *Sapajus* enclosure zone 5, the rock wall and rock ledge to the back left of the enclosure (U = 84, z = -2.121, p = 0.034, r = -0.51) and zone 7 (U = 18, z = -4.461, p <0.001, r = -1.08) were utilised significantly less than expected. Both East *Saimiri* (U = 55, z = -3.097, p = 0.002, r = -0.75) and West *Sapajus* (U = 57, z = -3.335, p = 0.001, r = -0.79) were observed in zone 1 (the large window and window sill where visitors can see into the indoor enclosure) significantly less than expected. Whereas the West *Saimiri* significantly underutilised zone 3 (U = 11, z = -2.655, p = 0.01, r = -0.89), zone 4 (U = 9, z = -2.929, p = 0.003, r = -0.98), zone 6 (U = 13, z = -2.433, p = 0.015, r = -0.81) and zone 7 (U = 0.0, z = -3.593, p < 0.001, r = -1.20). Observations of monkeys in zone 4 (large lower window and windowsill – can see into the cubicle research area) were rare or did not occur during sampling.

4.4.2 Heights occupied

The data presented in Figures 4.5 and 4.6 show the observed and expected values of heights occupied by the East and West groups of *Sapajus* and *Saimiri* in their indoor and outdoor enclosures. The percentage of *Sapajus* and *Saimiri* at each height level is relatively similar between the East and West groups, and they appear to be well distributed across the vertical space, though they were all observed significantly less than expected at ground level when indoors (Figure 4.5); East *Sapajus* (U = 85, z = -2.1, p = 0.036, r = -0.51) East *Saimiri* (ground, U = 34, z = -3.982, p < 0.001, r = -0.97; <2m, U = 84, z = -.086, p = 0.04, r = -0.51), West *Sapajus* (U = 18, z = -4.828, p < 0.001, r = -1.14), West *Saimiri* (U = 18, z = -2.049, p = 0.04, r = -0.68). Both groups of *Saimiri* were observed occupying heights of 2-4m (East, U = 64, z = -2.79, p = 0.005, r = -0.68; West, U = 15.5, z = -2.311, p = 0.021, r = -0.77) and > 4m (East, U = 22.5, z = -4.361, p < 0.001, r = -1.06; West, U = 4.5, z = -3.492, p < 0.001, r = 1.16) significantly less than expected (Figure 4.6 B, C). No significant differences were found between observed and expected values for the vertical distribution of East or West *Sapajus* (Figure 4.6 A, C) in their outdoor enclosures (p > 0.05).

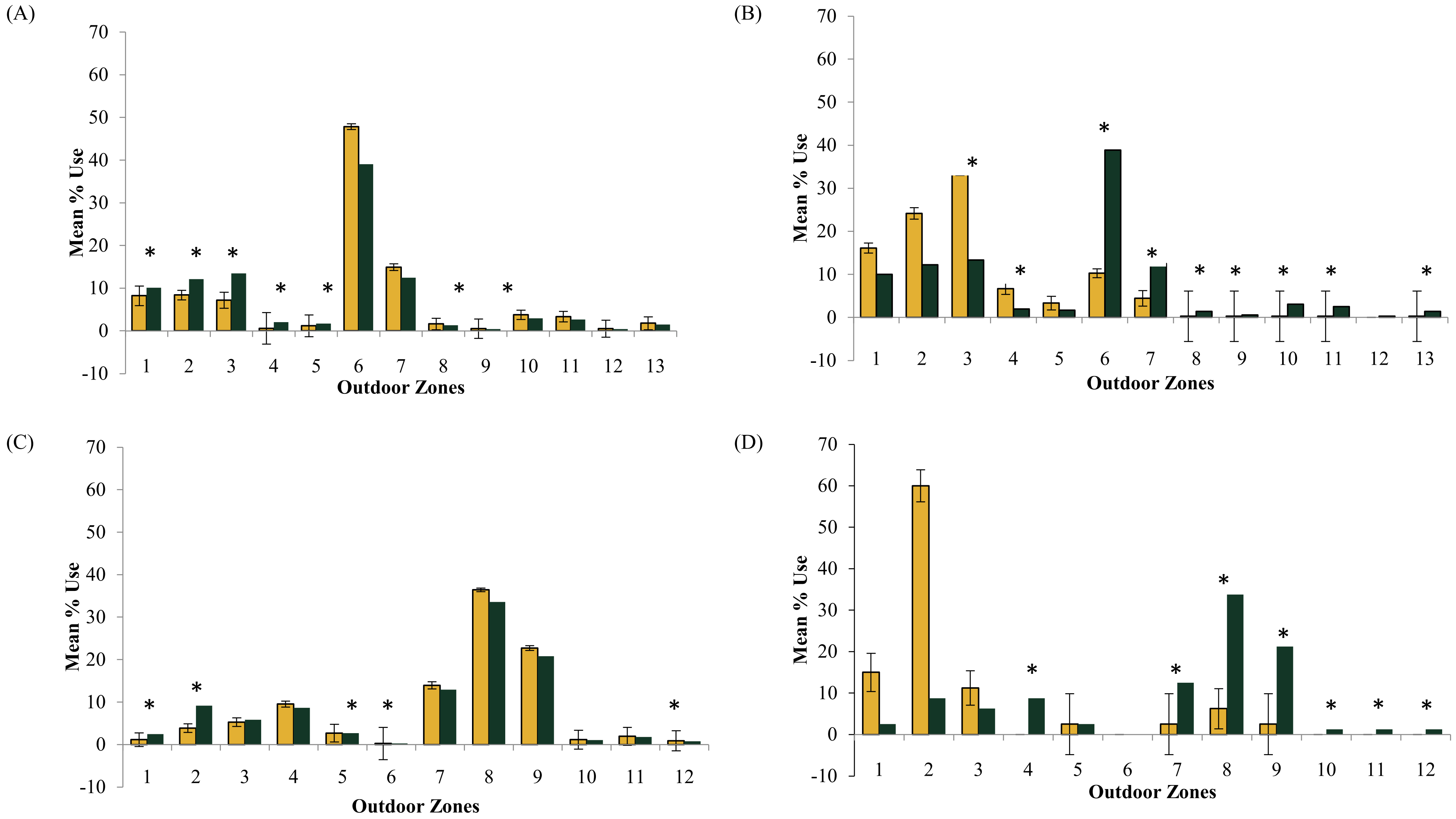


Figure 4.3 Zone use in East and West indoor enclosures (n=90) including ± S.E bars for **A)** East *Sapajus*, **B)** East *Saimiri*, **C)** West Sapajus and **D)** West Saimiri. An asterisk (*) indicates a significant difference between observed (yellow bars) and expected (green bars) values.

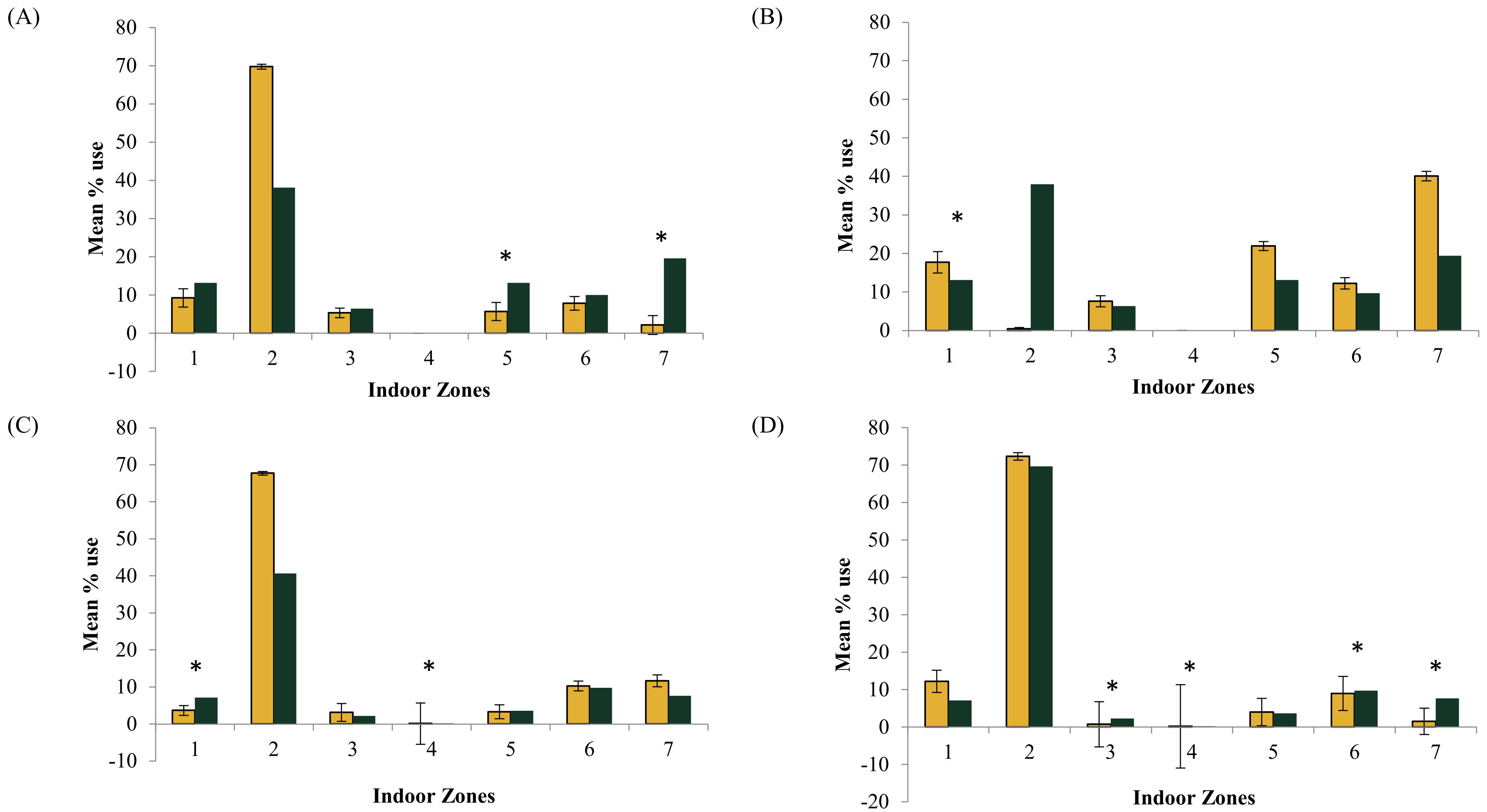


Figure 4.4 Zone use in East and West outdoor enclosures (*n*=90) including ± S.E bars for **A)** East *Sapajus*, **B)** East *Saimiri*, **C)** West *Sapajus* and **D)** West *Saimiri*. An asterisk (*) indicates a significant difference between observed (yellow bars) and expected (green bars) values.

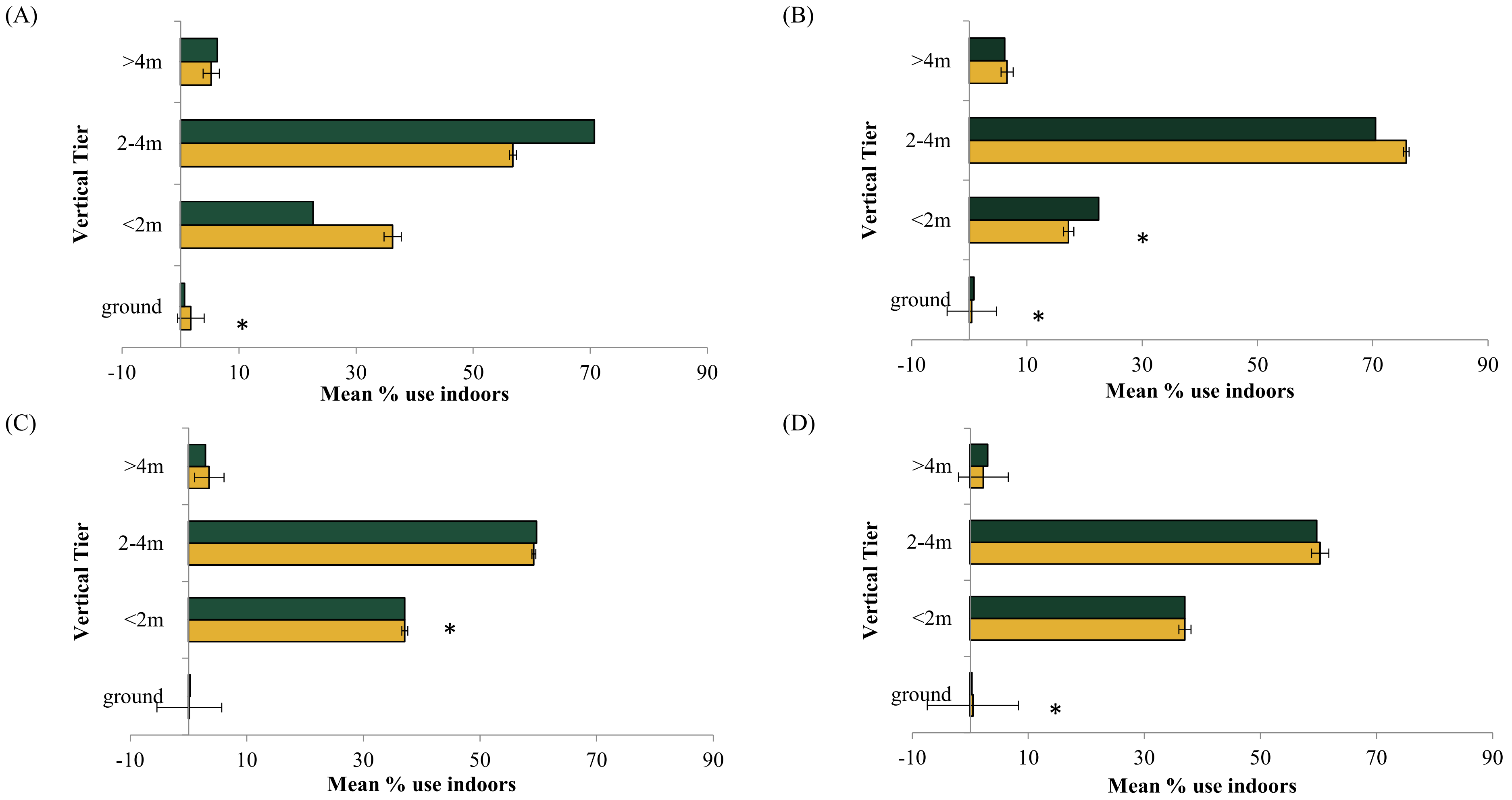


Figure 4.5 Use of four vertical tiers in the East and West indoor enclosures (*n*=90) including ± S.E bars for **A)** East *Sapajus*, **B)** East *Saimiri*, **C)** West *Sapajus* and **D)** West *Saimiri*. An asterisk (*) indicates a significant difference between observed (yellow bars) and expected (green bars) values.

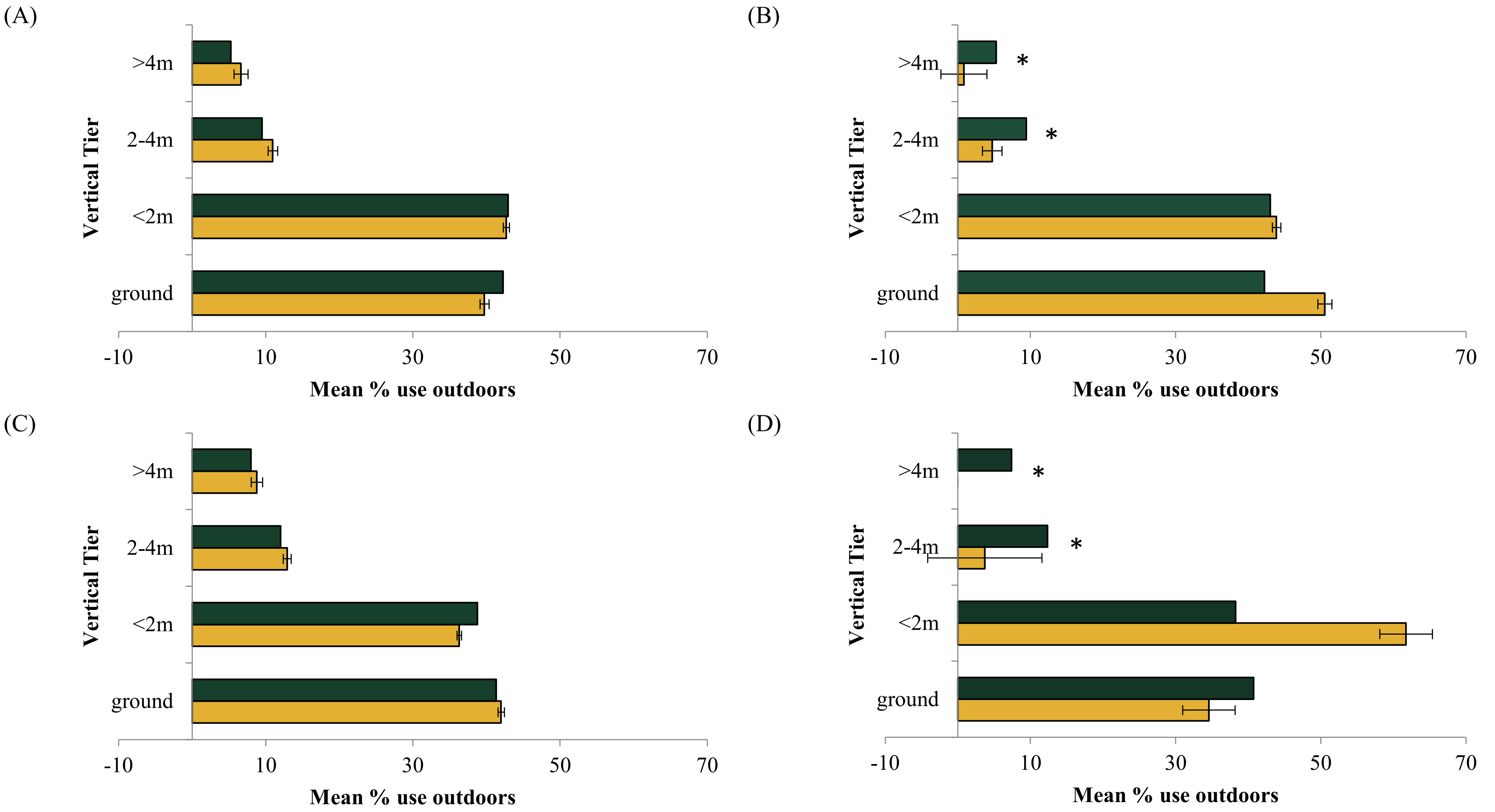


Figure 4.6 Use of four vertical tiers in the East and West outdoor enclosures (*n*=90) including ± S.E bars for **A)** East *Sapajus*, **B)** East *Saimiri*, **C)** West *Sapajus* and **D)** West *Saimiri*. An asterisk (*) indicates a significant difference between observed (yellow bars) and expected (green bars) values.

4.4.3 *Spread of participation index (SPI)*

Combined SPI values were calculated for zone use and heights occupied in order to determine 3D space use for all individuals, and the results indicate that overall *Saimiri* utilised less of the 3D space in their outdoor enclosures (East $M_{\mathrm{SPI}} = 0.33$, West $M_{\mathrm{SPI}} = 0.85$) than *Sapajus* (East $M_{\mathrm{SPI}} = 0.10$, West $M_{\mathrm{SPI}} = 0.06$), and the East groups utilised the 3D space in their indoor enclosures less (*Sapajus* $M_{\mathrm{SPI}} = 0.25$; *Saimiri* $M_{\mathrm{SPI}} = 0.23$) compared to the West groups (*Sapajus* $M_{\mathrm{SPI}} = 0.10$; *Saimiri* $M_{\mathrm{SPI}} = 0.04$). However, when considering individual differences within groups we can see that certain individuals better utilise the available space than others (Figure 4.7). If younger individuals required more space than adults, then we may have expected to see lower SPI values for juveniles and subadults. Linear regression analyses were performed to test whether there would be a relationship between age and enclosure use, based on combined SPI scores.

In the East groups, the results indicated that age could not predict indoor enclosure use for *Sapajus* ($b = 0.714$), explaining 11.3% of the variance, which was not significant, $R^2 = 0.113$, $F(1,16) = 1.914$, $p = 0.187$. The results also were non-significant for outdoor enclosure use ($b = 0.002$), where age explained 0% of the variance, $R^2 = 0.002$, $F(1,16) = 0.00$, $p = 0.997$. For the East *Saimiri*, age ($b = -0.608$) explained 16.8% of the variance in indoor enclosure, which was not significant, $R^2 = 0.168$, $F(1,16) = 3.023$, $p = 0.103$. Neither were the results for outdoor enclosure use ($b = 1.235$), which explained 17.1% of the variance, $R^2 = 0.171$, $F(1,17) = 3.305$, $p = 0.088$. The results for West *Sapajus* indicate that age could not predict indoor ($b = -0.069$) or outdoor ($b = 0.459$) enclosure use. Age only explained 0.2% of the variance for indoor enclosure use, $R^2 = 0.002$, $F(1,17) = 0.00$, $p = 0.846$, and 17.1% of the variance for outdoor enclosure use, $R^2 = 0.171$, $F(1,17) = 3.305$, $p = 0.088$, both of which were non-significant. Similarly for West *Saimiri* indoor ($b = 0.141$) enclosure use, age was found to explain 0.2% of the variance for indoor enclosure use, which was not significant, $R^2 = 0.002$, $F(1,8) = 0.014$, $p = 0.908$. However age significantly predicted outdoor enclosure use ($b = 2.498$) explaining 52% of the variance, $R^2 = 0.520$, $F(1,8) = 7.597$, $p = 0.028$. Furthermore, Wilcoxon's test confirmed significant differences between indoor and outdoor enclosure use in *Saimiri*, indicating avoidance behaviour. For East *Saimiri*, SPI values for enclosure use were significantly lower indoors ($Mdn = 0.13$) than outdoors ($Mdn = 0.35$), $z = -3.623$, $p < 0.001$, $r = -0.88$. Similarly, for West *Saimiri* SPI values for enclosure use were significantly lower indoors ($Mdn = 0.13$) than outdoors ($Mdn = 0.59$), $z = -2.668$, $p < 0.008$, $r = -0.89$.

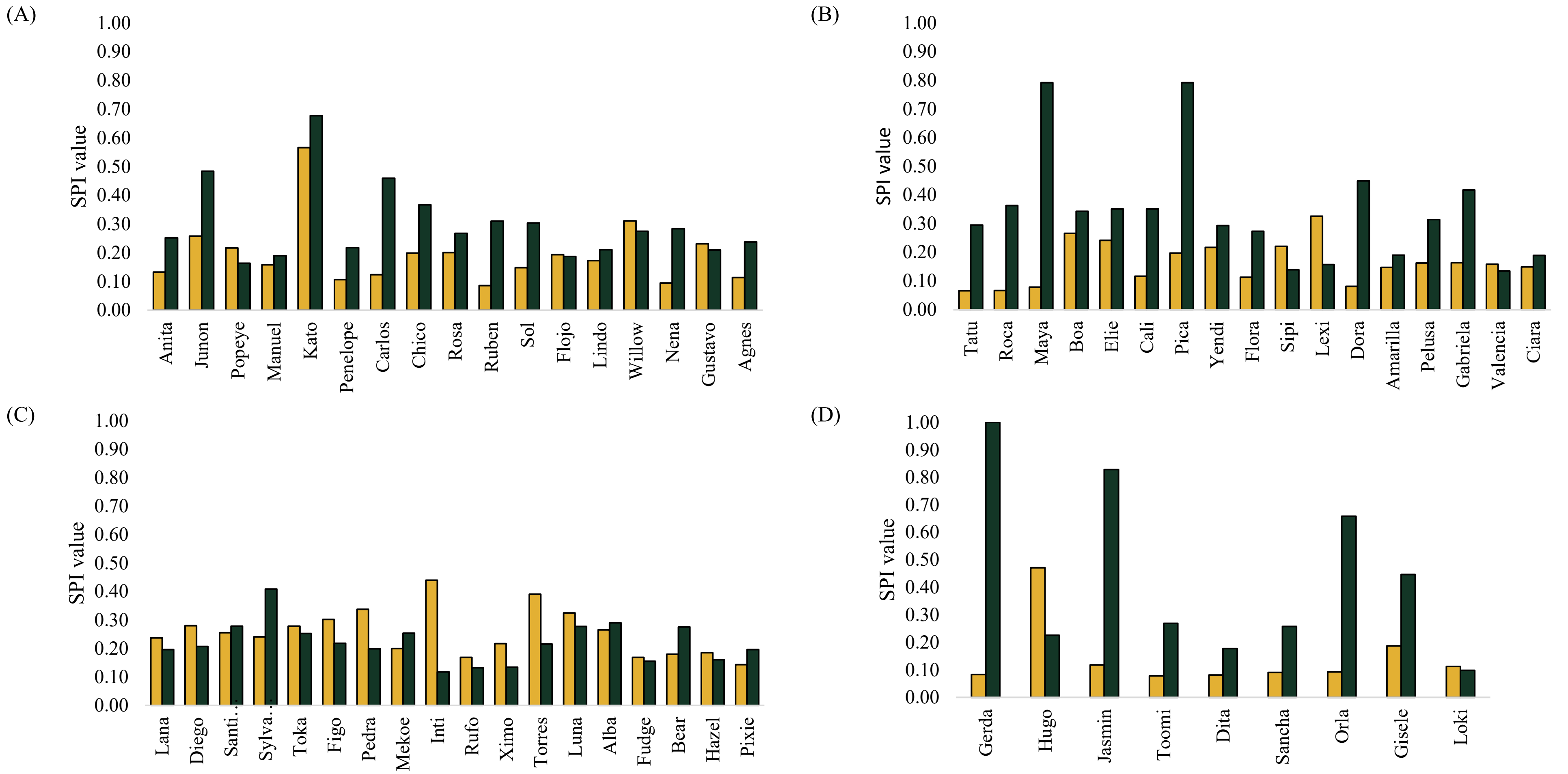


Figure 4.7 SPI for indoor (yellow bars) and outdoor (green bars) 3D enclosure use in East and West groups; **A)** East *Sapajus*, **B)** East *Saimiri*, **C)** West *Sapajus* and **D)** West *Saimiri*. Individuals are listed by age (oldest from left to youngest right). SPI values that are closer to 0 suggest maximum enclosure use (i.e. all zones and heights occupied equally) and a value of 1, minimum use of enclosure (i.e. only one zone or height occupied).

4.5 Discussion

Based on previous research of mixed-species associations in captivity (Leonardi et al., 2010; Buchanan-Smith et al., 2013) and the wild (Fleagle et al., 1981; Podolsky, 1990; Terborgh, 1983), I wanted to assess whether *Sapajus* and *Saimiri* were behaving as a true mixed-species group in relation to their space use (i.e. overlap in time and space due to social attraction). I predicted that if the monkeys were living as mixed-species groups then it was expected that they would occupy the same areas in their shared enclosures (though possibly at different height levels). However, the data did not fully support this prediction. Whilst East *Sapajus* and *Saimiri* were present in the same enclosures for 84% of scans (n = 90), which is in keeping with previous findings (~80% - see Buchanan-Smith et al., 2013), the results for West *Sapajus* and *Saimiri* showed a substantial decrease in the percentage of scans spent in shared enclosures (34%, n = 90) compared to previous data. Indicating that while there may be some social attraction between species in the East group, there is little evidence for it in the West groups. This decrease in occupying shared spaces by the West groups may be attributed to the change in the composition and number of individuals in the West *Saimiri* group from 15 individuals (2008–09), 10 individuals (2010) and 9 individuals (2015), providing an imbalance with the number of *Sapajus* (n=18). Generally, in the wild *Saimiri* troops are found in larger numbers 15-50 (Boinski, 1999; Jack., 2011) compared with *Sapajus* ~18 (Fragaszy et al., 2004; Jack, 2011 – see Chapter 1, Table 1.5). Group size varied as individuals were removed for husbandry purposes, to prevent intraspecific aggression and because a new and younger alpha male was introduced (see Buchanan-Smith et al., 2013).

When looking at the results of space use in the indoor enclosures, all of the groups with the exception of the East *Saimiri* were observed for a high percentage of scans, and more than what was expected, using zone 2 (the central structure compiled of tree log platforms and scaffolding, in a rectangular shape with criss-crossing sections on two levels ~2m and ~4m). East *Saimiri* showed preferences for the large windows at the front and back of their enclosure (zones 1 and 2), in addition to the rock wall and rock ledges towards the back of the enclosure (zones 5 and 6). This is likely why they were mostly observed at heights <2m-2-4m as this directly relates to the heights of the structures. Whereas in the outdoor enclosures there were distinct differences in space use by *Sapajus* and *Saimiri.* For instance, East and West *Sapajus* groups were observed more than would be expected, in the central zones (where tall trees were present) of their outdoor enclosures and appeared to use all available vertical space (though were mostly at lower levels <2m – see Figures 4.5, 4.6), which is in keeping with observations made in the wild (e.g. mid to lower levels of the main canopy - see Fleagle et al., 1981 see also Chapter 2). While East and West *Saimiri* groups were observed more than would be expected in peripheral zones of their outdoor enclosure with a high percentage of scans being in proximity to their indoor enclosure entrances (and also at lower levels <2m – see Figures 4.5; 4.6). This along with *Saimiri* being observed for a larger proportion of scans in their indoor enclosure compared to being in shared enclosures with *Sapajus* indicate that the two species are not behaving as a true mixed-species group. Furthermore, the separation between the two species could be an indicator that *Saimiri* are actively avoiding *Sapajus* and are possibly staying closer to indoor enclosure entrances as an escape option.

However, the habitual use and clustering of highly used areas has been reported in other studies of captive primates (Mallapur et al., 2005; Ogden et al., 1990; Ross et al., 2009; Stoinski et al., 2000), which indicates that enclosure use may also be dependent on functionality (i.e. locations with the greatest utility). Thus, alternatively, the difference in space use between the two species could be due to available substrates in shared enclosures being better suited to *Sapajus*. For instance, wild *Saimiri* tend to be found mostly in the forest understory, which is quite dense and well protected against aerial predators (e.g. Fleagle et al., 1981; Terborgh, 1983; Boinski, 1999). Therefore, large areas of wide open spaces (i.e. central 'tall tree' zones) would not be appropriate for *Saimiri*, whereas on the periphery there are more connecting evergreen bushes (see Figure 4.1; Table 4.1), which enable *Saimiri* to move through the enclosure without being out in the open where there may be perceived risk of predation (e.g. aerial predators). Thus, reinforcing the importance of providing structures and substrates that are appropriate for both species.

Furthermore, when examining the combined SPI for each individual, it is clear that there is a lot of variability in observed versus expected space use, however overall the data indicate that *Saimiri* use less of the available space compared to *Sapajus*. The age of individuals in relation to space use was also considered. Juveniles and subadults, though smaller than adults, are usually found to be more active and may have greater space requirements for physical development and play (Traylor-Holzer & Fritz, 1985; Wells & Turnquist, 2001). Therefore, it was predicted that both juveniles and subadults would use more space than adults, and as such may be more likely to overlap with heterospecifics. However, the data did not support this prediction as no significant relationship was found between age and enclosure use other than for the West *Saimiri* (i.e. younger individuals more likely to be in the outdoor enclosure), but this could have been due to the small sample size (9 individuals) compared with the other groups.

The use of specific areas in the shared outdoor enclosures observed in this study suggest some important points in relation to mixed-species groups in captivity. For example, having access to both indoor and outdoor enclosures is clearly not enough to enable two species that form mixed-species groups in the wild, to also form mixed-species groups in captivity. Especially if the substrates provided for the different species are in different locations, with few connectors between them (e.g. central tree zone is more appropriate to *Sapajus* and peripheral evergreen bushes are more appropriate to *Saimiri*), which will likely physically limit opportunities for the two species to mix. Living Links was built specifically with *Sapajus* and *Saimiri* in mind, and the design took into account a considerable number of factors that included ecological differentiation, different locomotor patterns and preferred support orientations and size (Poole, 1991; Buchanan-Smith et al., 2013). However the outdoor enclosure has changed over the years, with fewer horizontals linking vertical structures (central tree areas), no foliage on vertical structures (*Sapajus* are destructive foragers – see Terborgh 1983; Fragaszy et al., 2004), and larger open spaces between zones, as well as between indoor-outdoor enclosures, which may account for the lack of overlap in space use. Buchanan-Smith et al., (2013) found that enclosure furnishings affected interactions between species and as such deterioration of, or changes to furnishings at Living Links may confound research findings on social interactions and behaviour. Thus, while the findings from this chapter indicate that *Sapajus* and *Saimiri* were not behaving as a true mixed-species group due to their lack of proximity in time and space (partially prerequisite 3 – see also Figure 1.1), this may have been due to enclosure design, and as such care must be taken in subsequent chapters when drawing conclusions about the groupness of the mixed-species groups at Living Links.

The next chapter investigates behavioural synchrony at the group level, allowing for a thorough examination of the factors that might influence group behaviour in single-species and mixed-species groups. It explores further how often the monkeys choose to be in shared spaces compared to chance and irrespective of available food (i.e. not aggregating around a resource), and whether or not their behaviours are synchronised (i.e. coordinated in time and space).

5 BEHAVIOURAL SYNCHRONY

5.1 Abstract

Behavioural synchrony of individuals is one of the key features defining whether they form a group. It has been studied in group-living animals but has so far been limited to the study of single-species groups. Coordinated behaviour across group members is essential for maintaining spatial coherence and has important implications for individual survival and reproduction. I investigated to what extent individual activity budgets, habitat (spatial) constraints and group properties (e.g. groups size) may be influencing group behaviour, in two captive mixed-species groups of *Sapajus* and *Saimiri* at Living Links. Instantaneous scan sampling was used in order to capture group activities within the same time point. Observed synchrony (based upon 180 scans) across individuals was variable and analysed using linear models (LMs) and linear mixed models (LMMs). Overall synchrony was significantly greater than expected based on a randomly generated dataset where individuals behaved independently of each other. LMs identified no significant difference in *Sapajus* single-species and mixed-species behavioural synchrony, however there was a significant increase in synchrony for *Saimiri* single-species scans than in mixed-species scans. Furthermore, an LM identified that observed mixed-species behavioural synchrony was significantly lower than expected based on the average score of *Sapajus* and *Saimiri* behaviours. In other words, living in a shared enclosure did not lead to the monkeys synchronising their behaviours as may be expected of a true mixed-species group.

5.2 Introduction

Sociality can be advantageous for many group-living animals, as it provides opportunities for the exchange of useful information, such as locating more profitable foraging sites or detecting predators (see Chapter 1). Depending on the circumstances, individuals within a group will often need to make rapid decisions about where to move or what behaviour to perform. One efficient method of making such decisions is based on their social interactions and coordination with other group members (i.e. prerequisite 3 – behavioural coordination in time and space). This is particularly important when in an uncertain and potentially dangerous environment. This type of cohesive, coordinated and synchronised movement/ activities, otherwise known as 'collective behaviour' has been observed in a number of taxa, such as swarming ants, schooling fish (e.g. anchovies forming bait balls) and flocking birds (e.g. starling murmurations) to name a few (Couzin & Krause, 2003; Couzin, 2009; Sumpter, 2010). Individuals within these groups base their movement decisions on locally acquired cues, such as the position, or motion (or change in motion) of other group members (Couzin & Krause, 2003). However, each individual will typically only be able to use their relative local/proximal sensing ability (i.e. close enough for information exchange), which can be limited in larger and more dispersed groupings. As such, the groups are often composed of individuals that have different informational status and concurrently not all individuals will be aware of the informational state of others, such as whether they are knowledgeable about a pertinent resource, or a threat (Couzin & Krause, 2003; Couzin, 2009; Sumpter, 2010), which makes the collective response all the more remarkable.

There has been increased attention towards how animal social groups make collective decisions, and more specifically, how they achieve collective changes between activity states (e.g. from resting to moving, see Conradt & Roper, 2005; Couzin, Krause, Franks & Levin, 2005; Dostálková & Špinka, 2007; Conradt & List, 2008; Stueckle & Zinner, 2008; Sueur, Deneubourg & Petit, 2009). These coordinated changes between activities are crucial if individuals are to benefit from synchrony with other group members (Conradt, 1998; Ruckstuhl, 1999, King & Cowlishaw 2009), and are generally easier to identify than collective decisions occurring within a single activity state (e.g. the decision to change direction when moving) (Byrne, Noser, Bates & Jupp, 2009; Dyer, Johansson, Helbing, Couzin & Krause, 2009). Synchronised behaviour is broadly defined as individuals (in a dyad or group) performing the same activity at the same time and in the same place as others

(Louwerse, Dale, Bard & Jeuniaux, 2012; Duranton & Gaunet, 2016). However, it can be further characterised into three components:

> (1) temporal synchrony, occurs when individuals switch actions at the same point in time, these actions can be identical or different, the important feature here is the timing (Dostálková & Špinka, 2007; Duranton & Gaunet, 2015);
>
> (2) behavioural synchrony (also known as activity synchrony, behavioural matching or allelomimicry), takes place when individuals exhibit the same behaviour at the same time, such as foraging or resting (Chartrand & Bargh, 1999; Lakin, Jefferis, Cheng, & Chartrand, 2003; Gautrais, Michelena, Sibbald, Bon, & Deneubourg, 2007; Duranton & Gaunet, 2015);
>
> (3) local synchrony, is said to occur when individuals are in the same place at the same time, for example aggregating around a resource such as a watering hole (Bertram 1980; King & Cowlishaw, 2009; Duranton & Gaunet, 2015).

When considering synchronisation in practice, it is often difficult to distinguish between these three aspects, as more often than not it is likely that one would observe either a mixture of two or all three (Ramseyer & Tschacher, 2006; Duranton & Gaunet, 2016). For the purpose of this research I shall define behavioural synchrony as follows: when individual members of a group (West/East) perform the same activity in unison (during a scan) whilst in the same location (*Sapajus* indoor, *Saimiri* indoor, and outdoor enclosures) (Conradt & Roper, 2000; King & Cowlishaw, 2009; Fichtel, Zucchini & Hilgartner, 2011; Duranton & Gaunet, 2016).

There are a variety of taxa that form social groups, which differ in size, composition, permanence, and cohesion. As discussed previously (see Chapter 1), there are a number of advantages to group-living, such as reduced (*per capita*) predation risk (e.g. through shared vigilance or predator confusion), as well as costs to group-living, which tend to revolve around competition for resources. If an individual is to remain with its group then it should not go off alone and forage while the rest of the group is sleeping, nor should they stay behind and sleep when the rest of the group is on the move (Rook & Penning 1991; Conradt, 1998; Conradt & Roper, 2000). In general, to reap the benefits of group-living, animals will need to coordinate their activities to stay cohesive, and in order to maintain that cohesion, individuals will often need to engage in the same activity (Conradt & Roper 2000, 2003, 2007; King and Cowlishaw 2009; Rands, Cowlishaw, Pettifor, Rowcliffe & Johnstone, 2008; Fichtel et al., 2011). When all group members form a cohesive group, each individual will benefit from better protection against predators than a solitary individual and as a result improve their overall chances of survival (Conradt & Roper, 2000; Fernandez, Capurro & Reboreda, 2003; Duranton & Gaunet, 2016 – see also Chapter 1, Section 1.2). For instance, coordinating antipredator scans as a group is going to be more efficient than independent scanning, so long as the information (i.e. detection of a predator) is rapidly shared amongst all group members (Cords, 1990b; Hardie & Buchanan-Smith, 1997; Bednekoff & Lima 1998; Rodríguez–Gironés & Vasquez 2002; King & Cowlishaw, 2009).

Whilst there are clear benefits for groups to synchronise their behaviour, it can be costly to achieve for a number of reasons. Firstly, the 'activity budget hypothesis' (Demment & van Soest, 1985; Traylor-Holzer & Fritz, 1985) proposes that individual differences can impact on the group's ability to achieve synchrony, and activity budgets will differ based on age and sex as well as other physiological or morphological characteristics (Ruckstuhl, 1998; Stokke & du Toit, 2000; Ruckstuhl & Kokko, 2002). This individual variation influences individual states, such as increased nutritional demands and foraging bouts in pregnant females (Boinski, 1987b; Krebs & Kacelnik, 1991; Lee, 1994; Ruckstuhl, 1998; Conradt & Roper, 2000; Key & Ross, 1999; Barrett, Halliday & Henzi, 2006). Alternatively, the 'habitat constraints hypothesis' (Alexander, 1974; Bradbury & Vehrencamp, 1977; Moermond, 1979; Emlen, 1982) suggests that groups foraging in areas where food is scattered or in particularly dense and heterogeneous habitat, may find it difficult to maintain group synchrony (Nonaka & Holme, 2007; Vahl, van der Meer, Meijer, Piersma & Weissing, 2007; Kazahari & Agetsuma 2008). Finally, 'the group structure hypothesis' (Rowell, 1972; van Schaik & van Hooff, 1983) indicates that when group members move out of auditory range or become visually segregated (i.e. as a consequence of inter-neighbour distance), then there is likely to be a reduction in behavioural synchrony, due to a reduction in the opportunity to gain information from socially transmitted signals or cues (Couzin & Krause, 2003; Braune, Schmidt & Zimmermann, 2005; Cortopassi & Bradbury, 2006; Couzin, 2009; Sumpter, 2010). Consequently, when studying animal groups, it is important to consider how all three processes may contribute to variability in behavioural synchrony.

Group-level behavioural synchrony remains an understudied area within the non-human primate literature, with previous studies focussing on either coordinated action within dyads, or the influence that individuals have on group activities and movements, which is more akin to collective behaviour or to specific natural phenomena such as synchronised births (Boinski, 1987b; Agetsuma, 1995; Petit, Gautrais, Leca, Theraulaz & Deneubourg, 2009; Fichtel et al., 2011; King, Sueur, Huchard & Cowlishaw, 2011; Sueur, Deneubourg & Petit, 2012). These approaches sometimes ignore the complex and dynamic nature of the social space many group-living animals inhabit. However, a study by King and Cowlishaw (2009) examined group-level behavioural synchrony in two groups of chacma baboons (*Papio ursinus*), using a simple measure of species diversity (Simpson's Diversity Index, 1949, cited in King & Cowlishaw, 2009). Higher scores produced by this measure correspond to less behavioural diversity and greater behavioural synchrony. This measure enabled the authors to test hypotheses relating to behavioural synchrony based on ecological (e.g. habitat/spatial constraints), individual (e.g. individual activity budgets) and group (e.g. group structure) factors. Their findings identified a greater level of synchrony when groups were spread out over smaller areas (i.e. more cohesive), and they also identified a reduction in synchrony in larger groups. One study on brown capuchins (*S. apella*) had similar findings, as focal individuals would spend a higher proportion of time vigilant when there were a greater number of conspecifics within 10 metres (Hirsch, 2002). These findings emphasise how group size and group spread affects behavioural synchrony and may be indicative of the importance of proximity and group size in facilitating information exchange, via social monitoring and by increasing the perceptual availability of socially transmitted signals or cues.

Furthermore, despite the interest that ethologists have shown in the study of mixed-species groups, there have been few attempts to examine their behavioural synchrony. At the group level, simultaneous responses to alarm calls (Goodale, Ratnayake, & Kotagama, 2014) and synchronised foraging (Farine, Aplin, Garroway, Mann & Sheldon, 2014) have been observed in mixed-species bird flocks. A study on behavioural synchrony in a mixed-exhibit of communally housed chinstrap (*Pygoscelis Antarctica*) and gentoo (*Pygoscelis papua*) penguins at the Central Park Zoo, New York, USA, found that overall synchrony was greater within species than between species (Foerder, Chodorow & Moore, 2013). While the penguins did engage in the same behaviours (e.g. swimming, standing, preening and locomoting), there were clear differences between species, for instance *P. papua* had higher synchrony scores for standing, preening and locomoting than *P. Antarctica* or mixed-species (combined data). Although it may have been expected that interspecific synchrony would have been greater given that their captive environment is much smaller than their natural habitat, wild penguins typically divide themselves (by species) into separate colonies (Foerder et al., 2013). Therefore, when choosing a study species, it is important to consider whether they would naturally associate in the wild.

Within the primate literature, there are many studies that have investigated group foraging and vigilance (e.g. Clutton-Brock, 1975; Terborgh, 1983,1990; Whitesides, 1989; Cords, 1990b; Peres, 1993a; Hardie & Buchanan-Smith, 1997), though to my knowledge there are no known published studies that have investigated synchronised vigilance, foraging or other behaviours in mixed-species groups of non-human primates. However, a thorough search of the relevant literature did yield one article that specifically investigated interspecific behavioural synchrony between pigtailed macaques (*Macaca nemestrina*) and humans (Paukner, Anderson, Borelli, Visalberghi & Ferrari, 2005). The authors showed that *Macaca nemestrina* were sensitive to humans that were synchronising their behaviours with them, with the monkeys preferentially looking at the imitator and interacting more with them than with the experimenter who did not synchronise (Paukner et al., 2005). While these results are more conducive to recognising that non-human primates are able to understand when they are being imitated by an interspecific individual, the wider implications may indicate that non-human primates have the capacity to synchronise their behaviour(s) with other species. Indeed, we know that some monkeys are able to recognise and respond to the alarm calls of another species, such as Diana (*Cercopithecus diana diana*) and Campbell's monkeys (*Cercopithecus campbelli*) (see Coye, Ouattara, Zuberbühler & Lemasson, 2015). Therefore, the study of mixed-species behavioural synchrony could provide new insights that will enable us to better understand its proximate and ultimate causes.

This chapter investigates behavioural synchrony for two mixed groups of tufted brown capuchins (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) at the Living Links to Human Evolution Research Centre, RZSS, Edinburgh Zoo (hereafter Living Links). The neighbouring enclosures, containing separate populations of *Sapajus* and *Saimiri* (East and West groups), create an opportunity to examine inter- and intra-group dynamics not only between the two species but also between the two sides. Data collected from scan samples of both groups (see Chapter 3) allowed for the inspection of factors that contributed to within- and between-group behavioural synchrony. I asked to what extent observed variability in behavioural synchrony could be explained by individual activity budgets [Hypothesis, H1], habitat/spatial constraints [H2], group properties such as group-size and structure [H3]. These hypotheses are not mutually exclusive, and I outline my predictions for each in turn, based on previous literature.

To my knowledge, the study by King and Cowlishaw (2009), is the only previous published research of non-human primates that examines behavioural synchrony at the group level, which is why their work formed the basis for predictions. Their study identified individual activity budgets as a predictor for behavioural synchrony, with synchrony increasing with the proportion of pregnant females, and decreasing with the proportion of sexually swollen females. King and Cowlishaw (2009) attribute these differences in synchrony to factors such as differences in energy requirements for females in different sexual states (e.g. non-fertile, fertile females have lower energy requirement compared to pregnant and lactating females, see Altmann, 1980; Dunbar & Dunbar, 1988; Barrett et al., 2006), phenotypic variation and dominance hierarchies. With that in mind I wanted to examine phenotypic variation between the two species. Larger bodied animals will typically consume higher quantities of food but have lower energy requirements (per unit mass) compared to smaller animals (Bell, 1971; Geist, 1974; Fleagle & Mittermeier, 1980; Demment & van Soest, 1985; Kamilar & Pokempner, 2008). *Sapajus* ($M_{\text{adult male}}$ =3.0 kg; $M_{\text{adult female}}$ =2.4 kg - see Jack, 2007) are considerably larger than *Saimiri* ($M_{\text{adult male}}$ =0.74 kg; $M_{\text{adult female}}$ =0.64 kg - see Jack, 2007), and as such it would be expected that *Sapajus* will spend a higher proportion of time engaged in feeding/foraging compared to *Saimiri.* Therefore, based on these phenotypic differences between species, it is predicted that there will be a decrease in mixed-species behavioural synchrony compared to single-species (prediction 1.1). Alternatively, based on previous research of mixed-species groups of *Sapajus* and *Saimiri,* both species have been observed foraging and travelling together (e.g. Fleagle & Mittermeier, 1981; Terborgh, 1983; Podolsky, 1990), in which case if the two species were behaving as true mixed-species groups then synchrony is expected to be higher compared to single-species (prediction 1.2).

Within-species phenotypic variation, was also examined, as younger individuals typically have lower food requirements (owing to their smaller size) compared to adults, and are likely to stop foraging before older (larger) individuals, they are also more likely to be engaged in high-energy activities such as play (Traylor-Holzer & Fritz, 1985; Wells & Turnquist, 2001; Heise & Moore, 2003; Limmer & Becker, 2007). There is a higher proportion of adults compared to subadults and juveniles in each of the groups at Living Links (*Sapajus*: West=0.61, East=0.65; *Saimiri*: West=0.67, East=0.71, see also Chapter 3). Therefore, higher proportions of adults present in a scan is predicted to increase behavioural synchrony (prediction 2). In multi-male multi-female groups, sex may affect behavioural synchrony due to the different energy requirements between males and females (e.g. Altmann, 1980; Galdikas et al., 1981; Demment, 1983; Harrison, 1983; Ghiglieri, 1984; Iwamoto, 1987; Rodman & Mitani, 1987; Fragaszy, 1986, 1990; Robinson, 1981; Boinski, 1988a; Hiraiwa-Hasegawa, 1997; Key & Ross, 1999). The energetic demands on adult females (as mentioned above) arise predominantly from gestation, lactation, and rearing offspring (e.g. Altmann, 1980; Gautier-Hion, 1980; Lee, 1987; McFarland, 1997; Hiraiwa-Hasegawa, 1997; Key & Ross, 1999). Comparatively males will incur energy costs due to demands of sperm production, and competition for mates through mate guarding and male-male aggression (Leutenegger & Kelly, 1977; Kenagy & Trombulak, 1986; Baker & Dietz, 1993; Alberts, Altmann & Wilson, 1996). Though it must be noted that animals living in captivity will arguably have less energetic demands compared to their wild counterparts, due to food provisioning, hormonal control and limited to no threat(s) of predation (Melfi & Feistner, 2002). There is moderate sexual dimorphism in both *Sapajus* and *Saimiri*, and typically, males have been reported as engaging more frequently in vigilance behaviours, than to feeding and foraging compared to females (Boinski, 1986, 1988a, 1999; Fragaszy, 1986, 1990; Fedigan, 1993; Rose, 1994; Jack, 2011; Rylands & Mittermeier, 2013). Higher proportions of males present in a scan are therefore predicted to decrease behavioural synchrony (prediction 3). Reproductive state was not examined here due to there being only one breeding group (West *Saimiri*), and sex differences were only examined for the *Sapajus* groups because both *Saimiri* groups only contained one male.

Regarding enclosure (spatial) constraints, King and Cowlishaw (2009) identified spatial proximity (i.e. group cohesion), as a predictor for increased behavioural synchrony. The indoor enclosures at Living Links are considerably smaller (*Sapajus* 7m x 4.5m x 6m; *Saimiri* 5.5m x 4.5m x 6m) than the outdoor enclosure (900m^2), and so it is more likely that the same number of monkeys located indoors will be closer to each other on average than if they were outdoors. For instance, in terms of food patch configuration, where patches are closer together (i.e. in the indoor enclosures), individuals are expected to spend more time feeding and less time locomoting or foraging (e.g. picking at small items of food during locomotion). Comparatively, in the outdoor enclosures, food patches are more dispersed (e.g. food scattering – see Chapter 3 for husbandry routines), and individuals need to distribute their time more evenly across feeding, foraging and locomoting, leading to reduced levels of synchronised behaviour. Furthermore, if the groups are spread out over a larger area, then it is more difficult for individuals to maintain communication, thus behavioural synchrony is likely to decrease. Consequently, for the purpose of this research, the location of a group acted as a proxy measure of spatial proximity. The results from Chapter 4 on enclosure use found that the monkeys occupied very different areas of their outdoor enclosure, with *Sapajus* being generally more evenly distributed (though observed predominantly in central regions) than *Saimiri* who were mostly observed in peripheral areas, close to the entrance of their indoor enclosure. Therefore, it is predicted that *Saimiri* behavioural synchrony will be consistent across all locations (prediction 4), whereas *Sapajus* single-species, and mixed-species group behavioural synchrony is expected to increase when in the *Sapajus* indoor enclosures as the monkeys are likely to be more cohesive (prediction 5).

It is expected that behavioural synchrony will alter according to group properties, such as group size and whether observed in single-species or mixed-species groups. Group size can influence the likelihood of certain behaviours being performed, for instance, larger groups are generally more effective at avoiding predators through shared vigilance (i.e. more eyes and ears), which allows for a larger proportion of time to be dedicated to foraging/feeding (e.g. Cody, 1971; Hamilton, 1971; Krebs, MacRoberts & Cullen, 1972; Treisman, 1975a, 1975b; Pulliam, 1976; Bertram, 1978; Kenward, 1978; Elgar, 1989; Lima & Zollner, 1996 – see also Chapter 1). Previous findings in groups of wedge-capped capuchins (*Cebus olivaceus* - de Ruiter, 1986), degus (*Octodon degus* - Ebensperger, Hutado and Ramos-Jiliberto, 2006) and eastern grey kangaroos (*Macropus giganteus* – Pays et al., 2009), suggest that foraging behaviour increases with group size. Contrary to this, Hirsch's (2002) study on wild groups of *Sapajus* found that the rate of individual vigilance was positively correlated with group size. This difference in the rate of vigilance was partially attributed to social monitoring, whereby subordinate individuals are directing a proportion of their vigilant behaviours toward dominant individuals (Chance, 1967; Haude, Garber & Farres, 1976; Caine & Marra, 1988; Rose & Fedigan, 1995; Treves, 1999; Hirsch, 2002; Pannozzo, Phillips, Haas & Mintz, 2007). It is suggested that this type of directed vigilance enables subordinate individuals to avoid agonistic interactions. Therefore, in larger groups there will likely be greater behavioural diversity in relation to hierarchy, with greater vigilance in lower ranking individuals (i.e. social monitoring) and foraging in higher ranking individuals, and as such it is predicted that *Sapajus* behavioural synchrony will decrease with group size (prediction 6). Interestingly, comprehensive field studies on *Saimiri* spp. (*S. boliviensis*, Manu, Peru - largest average group size ≥50 individuals; *S. oerstedii*, Corcovado, Costa Rica - average group size ≤40 individuals; and *S. sciureus*, Raleighvallen Suriname - smallest average group size ≤25), did not find the rate of vigilance to be affected by group size in any of the regions, despite differences in habitat type and social organisations (Boinski, 1999; Boinski et al., 2003). However, in a variety of captive settings, *S. sciureus* have been found to interrupt their foraging bouts in order to monitor other members of their group more often than tamarins (*Saguinus labiatus*), who under the same conditions monitored more non-social aspects of their environment (Caine & Marra, 1988). This difference in vigilance was attributed to the differences in social organisation of the monkeys; *Saimiri* live in larger multi-family groups that are hierarchical, whereas *Saguinus* typically live in smaller family groups). Therefore, it is predicted that behavioural synchrony in *Saimiri* will decrease with group size, as the presence of more individuals may increase the likelihood of social monitoring (prediction 7).

Individuals benefitting from the antipredator actions (i.e. shared vigilance) of others when in larger groups, is also applicable in mixed-species groups (e.g. birds –Thompson & Barnard, 1983; gazelles, Fitzgibbon, 1990; tamarins – Hardie & Buchanan-Smith, 1997). For instance, the ability of different species to adjust their vigilance patterns, and respond to the alarm/warning calls of another species, indicates that they are including the presence of another species within their possible notion of group size (Lima, 1995; Hardie & Buchanan-Smith, 1997). Furthermore, it must be noted that the benefits of forming larger groups by associating with another species may be asymmetrical between the species (Alexander, 1974; Terborgh, 1983; Gochfield & Burger, 1994; Lee, 1994; Lima, 1995; Hardie & Buchanan-Smith, 1997). Therefore, if *Sapajus* and *Saimiri* are sharing vigilance and behaving as a true mixed-species group then it would be expected that increased group size would result in higher behavioural synchrony (prediction 8.1). But, if increasing group size leads to greater behavioural diversity such as *Saimiri* engaging more frequently in social monitoring (i.e. increased vigilant behaviours) towards the larger more dominant *Sapajus* (due to their presence or if there is a higher proportion of *Sapajus* compared to *Saimiri*) then mixed-group synchrony is expected to decrease (prediction 8.2).

Lastly, ecological conditions such as weather, time of day and outdoor temperature were considered as potential contributors to behavioural synchrony, although the direction of the effect is unspecified (prediction 9). An animal's behaviour can be strongly influenced by the environment in which it lives, not just in terms of habitat, food distribution and abundance, but also by time of day, seasonality and climate (e.g. Kummer, 1971; Iwamoto & Dunbar, 1983; Terborgh, 1983; Henzi, Byrne & Whiten, 1992; Brent, Koban & Evans, 2003). For instance, in the wild, while rainfall and temperature may directly impact the activity patterns of animals, it can also have an indirect effect (i.e. plant growth) in relation to food availability (Henzi et al., 1992). Furthermore, captive studies on different primate species have found that weather, outdoor temperature and or time of day impact behaviour and activity budgets. O'Neill (1994) found that rhesus macaques (*Macaca mulatta*) would spend more time indoors when temperatures were <3.9ºC, and outdoors when temperatures were ≥32ºC. Similarly, Suchi and Rothe (1999) noted that common marmosets (*Callithrix jacchus*) tended to sleep in their outdoor enclosure when the temperature was high and the wind was low. Weather was found to affect both behaviour and the distribution of *Sapajus*, with colder weather (<10ºC) reducing overall activity levels, and warm weather (>15ºC) increasing foraging behaviours and group dispersal (Ross & Giller, 1988). Comparatively, weather (i.e. sunny, overcast) was not found to impact behaviours of ring-tailed lemurs (*Lemur catta*) apart from when it was raining (increase in resting), however time of day did (Goodenough, McDonald, Moody & Wheeler, 2019).

By studying a range of factors such as: ecological/spatial (e.g. enclosure, weather, temperature), group properties (e.g. single/mixed-species, group size) and activity budgets that could influence behavioural synchrony we may better understand the proximate and ultimate causes of mixed-species group behaviour. *Sapajus* and *Saimiri* are known to form associations in the wild and are often referred to as mixed-species groups. Thus, if the two species at Living Links are indeed forming true mixed-species groups then it is expected that there will be high rates of cohesion and synchrony.

5.3 Methods

5.3.1 Subjects

Study animals were the two groups (East and West) of *Sapajus* and *Saimiri* at Living Links. Both groups of *Sapajus* contained adults, subadults and juveniles of both sexes, whereas both *Saimiri* groups contained only one adult male, with the rest being a mix of adult and sub-adult (1 juvenile in the West) females. At the start of the study (June 2015) there were 17 individuals for both *Sapajus* and *Saimiri* groups in the East exhibit, 18 individuals in the West *Sapajus* and 9 in West *Saimiri*; and additional 4 infants were born during the study in the West *Saimiri* group, though they were not included in data collection (Table 5.1 summarises the group compositions). Each monkey could be individually identified by their facial characteristics and additional artificial aids for *Saimiri* (chain collars with colour coded beads). For more specific details on subjects and housing and husbandry please refer to Chapter 3 (Section 3.2.2).

Table 5.1 *Group compositions (male = ♂; female = ♀) of the monkeys at Living Links (April-August 2015).*

Group	Species	Adult ♂	Adult ♀	Sub-adult ♂	Sub-adult ♀	Juvenile ♂	Juvenile ♀
East	*Saimiri*	1	11	-	5	-	-
	Sapajus	6	5	1	1	1	3
West	*Saimiri*	1	6	-	1	-	1
	Sapajus	7	4	1	2	2	2

5.3.2 Design & Procedure

Data were collected over 19 days, during June-August 2015 by G. Badihi, (see Chapter 3, Section 3.4 for details on inter-observer reliability). All observable monkeys (both *Sapajus* and *Saimiri*) were sampled in each scan, with the exception of the West *Saimiri* infants that were born later in the study (August 2015). Scans were collected for all group members within 15-minute intervals for either West or East (see Leonardi et al., 2010). We recorded each individual in the indoor enclosures first, choosing individuals from left to right, then individuals in the outdoor enclosure. If an individual was not observed during a scan then that individual would be recorded as out-of-sight. Observations were taken from one of the three public viewing platforms: the West platform, the central platform or the East platform (see Figure 5.1). Recording took place throughout the week (Monday-Sunday) between

09.00 and 17.00, accumulating a total of 180 scans divided equally between the West and East groups. An average of 9.47 scans were made on any day (min=4; max=14; *n*=19 days). We avoided collecting data during cubicle research testing times (Mondays, Tuesdays, Thursdays and Fridays: 11.15-12.45 and 14.15-15.45), so that all individuals had the potential to be sampled. During scans a monkey could be inside or outside. Time of observation was recorded, as well as location (see Figure 5.1), weather conditions (see Chapter 3, Table 3.4) and behaviours (see Chapter 3, Table 3.3). The temperature at the time of the scan was recorded retrospectively from the Met Office www.metoffice.gov.uk/ using the closest weather station as a reference point (Edinburgh Airport). While there is a discrepancy with the location of temperature, which may mean a slight difference between the recorded and actual temperature at the research site, relative variation throughout the sampling periods should be reliable.

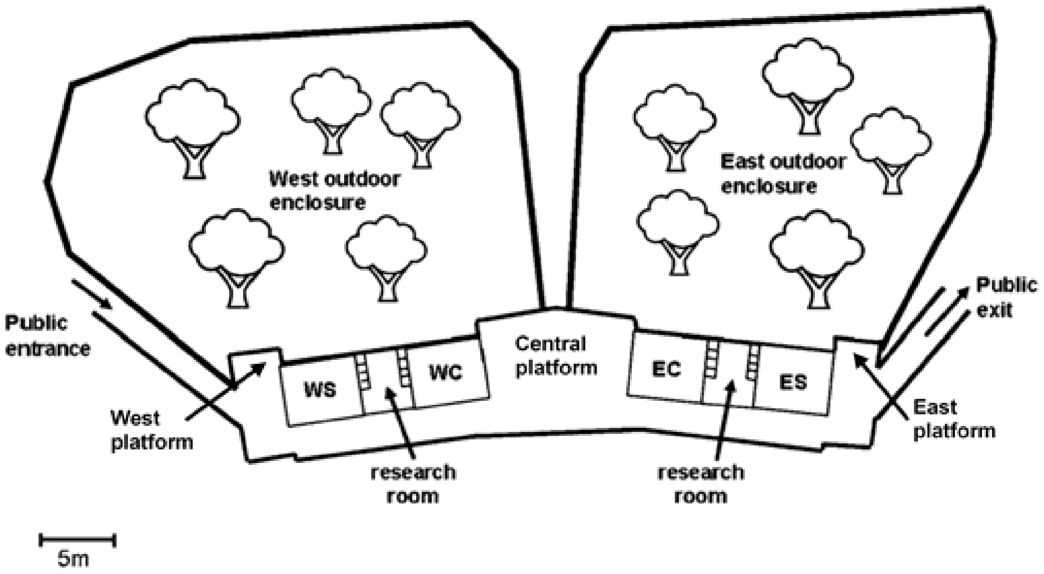


Figure 5.1 Schematic diagram (approximately to scale) of the Living Links to Human Evolution Research Centre, RZSS, Edinburgh Zoo (taken and adapted from Leonardi et al., 2010).

Although a group is characterised by two or more individuals (see Chapter 1), for the purpose of analysing group-level effects, a group was defined here as three or more monkeys (includes both *Sapajus* and *Saimiri*) present in the same enclosure (i.e. West/East *Sapajus* indoor, West/East *Saimiri* indoor and West/East outdoor). A minimum of three individuals is required because with two individuals you would either get a value of one (maximum synchrony) or zero (no synchrony), constraining the analyses. Thus, scan samples where one, two or no individuals were present at the location (e.g. indoor/outdoor) were not included in the analysis for behavioural synchrony. Mixed-species group scans (N_{EastIn} = 58, $N_{EastOut}$ = 86; N_{WestIn} = 76, $N_{WestOut}$ = 69) and single-species group scans for *Sapajus* (N_{EastIn} = 29, $N_{EastOut}$ = 85; N_{WestIn} = 74, $N_{WestOut}$ = 68) and *Saimiri* (N_{EastIn} = 77 (*Saimiri* indoor), N_{EastIn} = 32 (*Sapajus* indoor), $N_{EastOut}$ = 51; N_{WestIn} = 87 (*Saimiri* indoor), N_{WestIn} = 2 (*Sapajus* indoor); $N_{WestOut}$ = 18) were included in the final analysis.

5.4 Data Analysis

In order to understand what affects behavioural synchrony in mixed-species groups of *Sapajus* and *Saimiri*, I assessed synchrony across a number of activity categories (see Chapter 3, Table 3.3) between and within the two groups (West and East). Specific techniques for quantifying synchrony have been devised to examine differences in behavioural synchrony for particular activities between certain individuals or subgroups, such as males and females or juveniles and adults (Engel & Lamprecht, 1997; Ruckstuhl, 1999; Dunbar & Shi, 2008; Beauchamp, 2009). However, these techniques focussed more on the likelihood of concurrence between a focal animal and its neighbour(s) performing a particular behaviour.

However, this would not work with my data, as I was focussing on group-level behavioural synchrony across all individuals and behaviours. Thus, the degree of behavioural synchrony (*BS*) was calculated using a simple index that measures diversity in categorical data, as described by King and Cowlishaw (2009) ‘the Simpson’s Diversity Index’ (see Peet, 1974):

$$BS = \sum_{i=7}^{S} \frac{n_i \, (n_i - 1)}{N \, (N - 1)}$$

where n_i is the total number of observable individuals engaged in a specific behaviour, and N is the total number of individuals in view, for i=7 categories. Behavioural synchrony scores near zero indicate that the groups were heterogeneous with respect to behaviour and could therefore be considered asynchronous, while scores closer to 1 indicate more homogeneity and therefore better synchrony.

To examine whether variability in behavioural synchrony in my sample was greater than would be expected by chance, I compared my data with a randomly generated dataset in which each monkey's behaviour was independent of the rest of the group (this was calculated for mixed-species and single-species data). Each monkey was assigned a probability of performing a behaviour, based on the mean proportion of time monkeys were engaged in each of the seven behavioural categories: (1) locomoting, (2) vigilant, (3) resting, (4) foraging, (5) play, (6) grooming and (7) aggression (see Chapter 3, Table 3.3), derived from scan data (*N*=90) for each group (West and East). I then simulated each individual's activity 90 times for *N*=61 monkeys (in Excel 2016), which was equivalent to the number of scan observations conducted for these two groups. Once the scores for behavioural synchrony were calculated, the variation found in both the real and randomly generated data were compared in R using a Levene's test.

Table 5.2 *The Predictions for behavioural synchrony (BS) based on the three broader theoretical concepts (habitat/spatial constraints, group properties and activity budgets), within and between Sapajus and Saimiri groups, ranked in order of predictive importance (e.g. A=high importance, E=low importance) in preparation for multi-linear regression analyses. See text for full details of the literature leading to predictions.*

Rank	Prediction	Reference
Single-species		
A	**Habitat/spatial constraints:** *Saimiri*: BS will be consistent irrespective of enclosure (prediction 4) *Sapajus*: BS will be greater in indoor enclosures when the monkeys are likely to be more cohesive than in outdoor enclosure (prediction 5)	Nonaka & Holme (2007); Vahl et al. (2007); King & Cowlishaw (2009); see also Chapter 4
B	**Group properties:** *Saimiri* & *Sapajus*: As larger groups will have a more varied group composition, we may expect a reduction in BS (prediction 6 & 7)	Fleagle & Mittermeier (1980); De Ruiter (1986); Caine & Marra (1988); Hirsch (2002)
C	**Activity budgets:** *Saimiri* & *Sapajus*: Higher proportion of adults present in a scan will lead to increased behavioural synchrony (prediction 2)	Traylor-Holzer & Fritz (1985); Wells & Turnquist (2001); Heise & Moore (2003); Limmer & Becker (2007)
D	**Activity budgets:** *Sapajus*: Higher proportion of males present in a scan will lead to a decrease in group behavioural synchrony (prediction 3)	Altmann (1980); Boinski (1999); Jack (2011); Rylands & Mittermeier (2013)

Table 5.2 *continued.*

Single-species		
E	**Habitat/spatial constraints:** weather, outdoor temperature and time of day will have an effect (direction unspecified) on BS (prediction 9)	Ross & Giller (1988); O'Neill (1994); Suchi & Rothe (1999); Goodenough et al. (2019)
Mixed-species		
A	**Habitat/spatial constraints:** BS higher in shared (*Sapajus*) indoor enclosures when the monkeys are likely to be more cohesive than in outdoor enclosures (prediction 4)	Nonaka & Holme (2007); Vahl et al. (2007); King & Cowlishaw (2009); see also Chapter 4
B	**Activity budgets:** If phenotypical differences in energy requirements apply, then BS is expected to decrease (prediction 1.1) If behaving as a single group then due to shared vigilance, both species are more likely to be engaged in the same behaviours (e.g. feeding/foraging) resulting in higher BS (prediction 1.2)	Bell (1971); Geist (1974); Fleagle & Mittermeier (1980); Demment & van Soest (1985); Kamilar & Pokempner (2008)
C	**Group properties:** Increased group size will increase behavioural synchrony if the species are behaving as a group (prediction 8.1) Decreased BS if not behaving as a group; *Saimiri* social monitoring of *Sapajus* (prediction 8.2)	Fleagle & Mittermeier (1980); De Ruiter (1986); Caine & Marra, (1988); Hirsch (2002); Chance (1967); Haude et al. (1976); Caine & Marra (1988); Rose & Fedigan (1995); Treves (1999); Hirsch (2002); Pannozzo et al. (2007)
D	**Habitat/spatial constraints:** weather, outdoor temperature and time of day will have an effect (direction unspecified) on BS (prediction 9)	Ross & Giller (1988); O'Neill (1994); Suchi & Rothe (1999); Goodenough et al. (2019)

To assess what variables could be contributing to behavioural synchrony in mixed-species and single-species groups, linear (LM) and linear mixed (LMM) models were developed. Behavioural synchrony scores were initially assessed with histograms (eyeballing the data), and were found to follow a relatively normal distribution, therefore logarithmic transformations were not required. The Enter method was adopted to examine the contribution of a range of factors including: group (categorical: East/West); species (categorical: *Sapajus*/*Saimiri*); location (categorical: *Sapajus* indoor, *Saimiri* indoor and outdoor [for mixed-species *Saimiri* indoor was not included]); weather (categorical: clear, light clouds, cloudy, overcast, rain, wind); outdoor temperature (continuous); time (continuous); proportion adult (count); proportion *Sapajus* (count) only for mixed-species scans; proportion male (count) *Sapajus* only; and group size at the time of observation (count) (see Table 5.2). Predictor variables were first examined for collinearity using a Variance Inflation Factor (VIF) test, to which no problematic correlations were identified (i.e. no values exceeded 5; see James, Witten, Hastie & Tibshirani, 2013). The criterion for entry into the model was $p<0.05$, however if results are marginally significant $p<0.1$ then interactions between variables of interest were examined. Significant contributions to the models were assessed using an F-test. To test whether some behaviours were more likely to have contributed to the measure of behavioural synchrony, the relationship between synchrony scores and the frequency of monkeys performing each behaviour was examined with a correlation matrix (using Kendall's tau to correct for multiple comparisons); correlations between the frequency of all other behaviours are also reported.

All statistical tests were performed using the software package R (version 3.6.3) in the RStudio environment (R Core Team, 2020; RStudio, 2020 – see code for all R analysis here https://osf.io/ydceb/). Figures were produced using Microsoft Excel 2019.

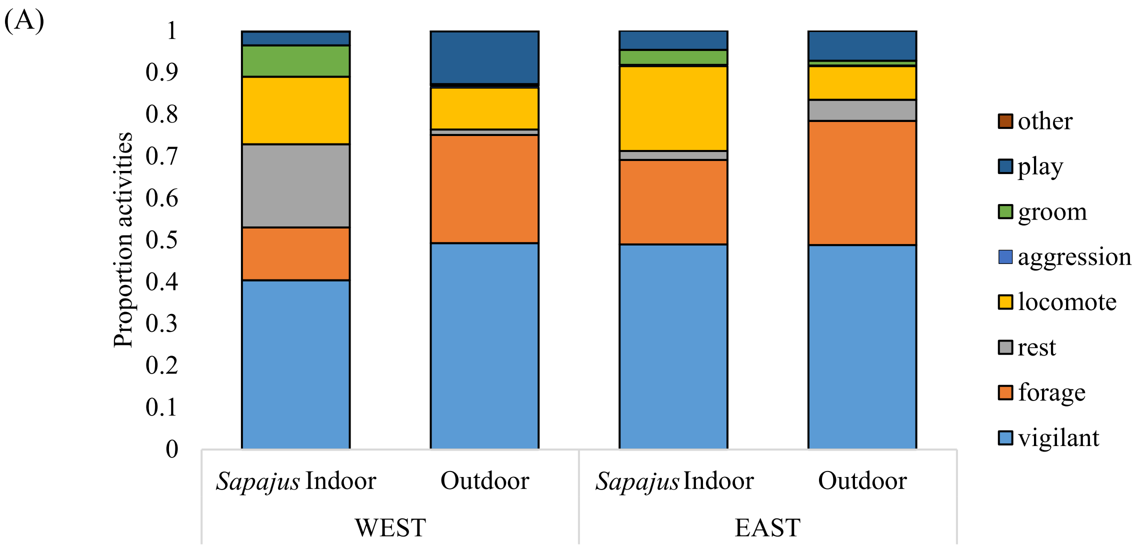
5.5 Results

The proportion of scans where at least one monkey was present in each location (i.e. *Saimiri/Sapajus* indoor or outdoor enclosures) was generally quite high (≥0.69), with the exception of the West *Saimiri* who were only present inside the *Sapajus* indoor enclosure for three scans out of a potential 90 (see Table 5.3). Such a low proportion would result in low statistical power and increase the likelihood of Type I errors if included in further analyses (Rusticus & Lovato, 2014), and as such the data were only included as part of the overall mixed-species analyses. The proportion of monkeys engaged in each behaviour (see Chapter 3, Table 3.3) in relation to their location (i.e. *Saimiri/Sapajus* indoor or outdoor enclosures) are shown in Figure 5.2, whereby vigilance was the most frequently observed behaviour followed by foraging, locomoting and rest. Overall, vigilance does not appear to change much for either of the monkey groups regardless of whether they were in the indoor or outdoor enclosures. That said, the East *Saimiri* spend a higher proportion of time being vigilant when they are in the *Sapajus* indoor enclosure, compared to their own indoor enclosure (see Figure 5.2 B), which may indicate social monitoring of *Sapajus*. Foraging is higher for *Sapajus* when in the outdoor enclosures compared to when they were observed indoors, however location does not seem to have an impact for the *Saimiri* groups (Figure 5.2B).

Table 5.3 *Proportion of scans (n=90 scans for the West and East groups) with at least one monkey present in each enclosure.*

	Sapajus		*Saimiri*		
	Indoor	Outdoor	Indoor	*Sapajus* Indoor	Outdoor
West	0.98	0.84	0.98	**0.03**	0.21
East	0.75	1.00	1.00	0.69	0.69

A higher proportion of males present (*Sapajus* only) in a scan was predicted to decrease group synchrony (prediction 2), as it was expected that males would be more likely to be performing vigilant behaviours compared to females, who were expected to be engaged in foraging. However, it was found that both males and females in each group spent an equally high proportion of observations in vigilant behaviours both indoors (West: male=0.41, female=0.40; East: male=0.47, female=0.53) and outdoors (West: male=0.51, female=0.48; East: male=0.50, female=0.48), and relatively low proportions foraging both indoors (West: male=0.13, female=0.12; East: male=0.17, female=0.26) and outdoors (West: male=0.24, female=0.29; East: male=0.30, female=0.29). Therefore, based on these findings a high proportion of males in a scan may actually increase group synchrony.



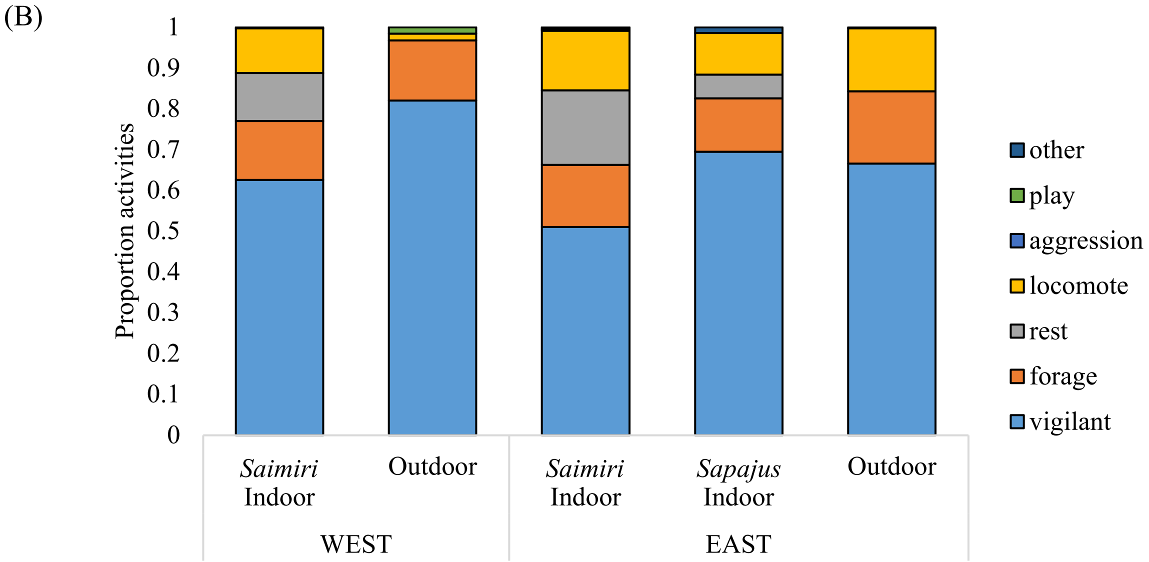


Figure 5. 2 Proportion of (A) *Sapajus* (West: indoor=76 scans, outdoor=68; East: indoor=28 scans, outdoor=85 scans) and (B) *Saimiri* (West: indoor (*Saimiri*)=87 scans, indoor (*Sapajus*)=NA (only 3 scans), outdoor=18; East: indoor (*Saimiri*)=77 scans, indoor (*Sapajus*)=34, outdoor=51 scans); behaviours in the indoor and outdoor enclosures based on individual activity budgets from a total of 180 scans for the West and East groups. The data for West Saimiri in the *Sapajus* indoor enclosure were not included due to only being present in three scans.

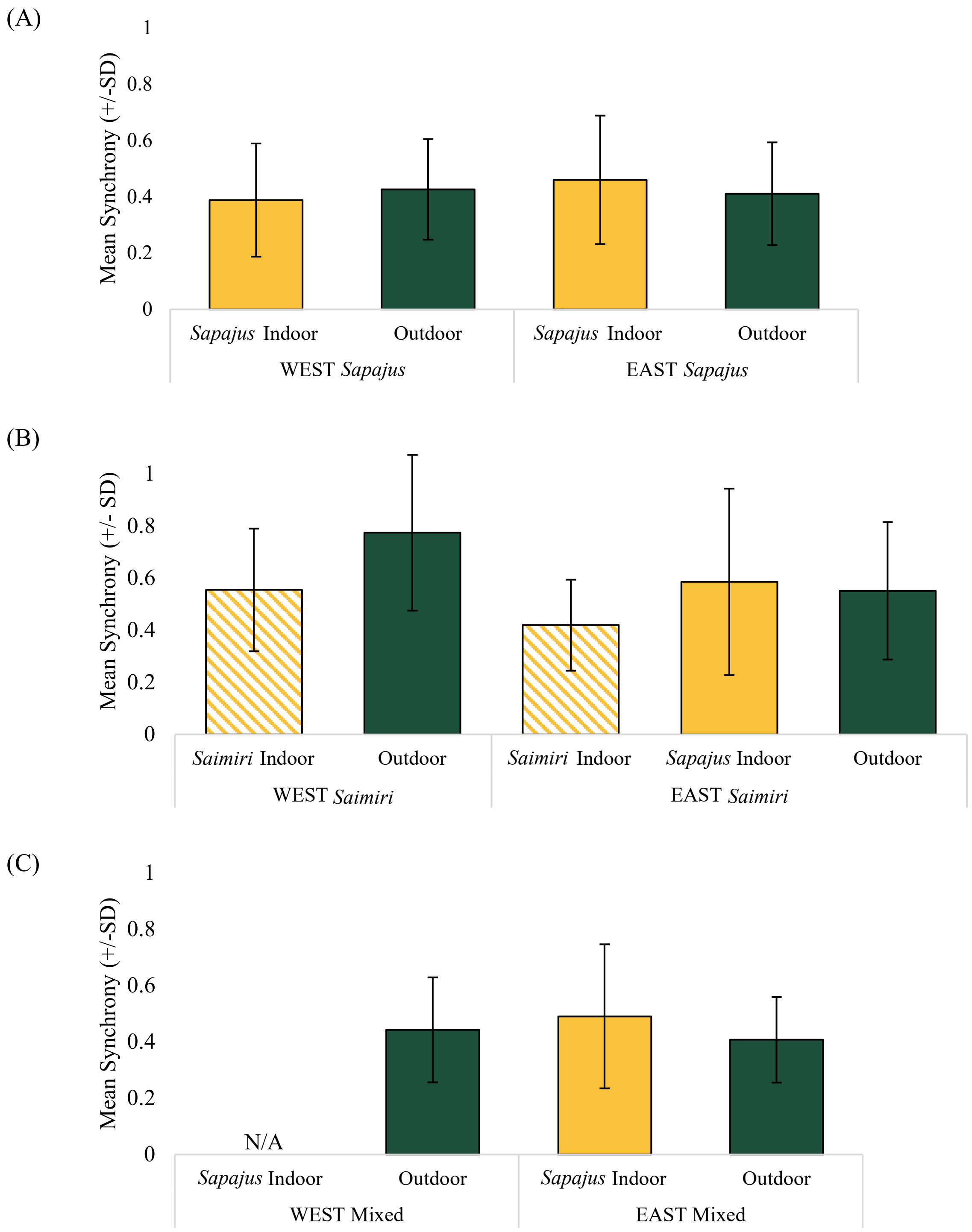


Figure 5.3 Mean indoor and outdoor behavioural synchrony scores (± SD) for (A) *Sapajus* single-species (West: indoor=76 scans, outdoor=68; East: indoor=28 scans, outdoor=85 scans) (B) *Saimiri* single-species (West: indoor (*Saimiri*)=87scans, indoor (*Sapajus*)=NA (only 3 scans), outdoor=18; East: indoor (*Saimiri*)=77 scans, indoor (*Sapajus*)=34, outdoor=51 scans); (C) and mixed-species (West: indoor= NA (only 3 scans), outdoor=34; East: indoor=43 scans, outdoor=64scans). Behavioural synchrony was calculated if ≥3 monkeys present in a scan.

If behavioural synchrony was affected by spatial constraints, then we may expect the monkeys to be more synchronised when observed in the smaller indoor enclosures (prediction 4). While mean synchrony scores were found to be slightly higher for East *Sapajus* in their indoor enclosure ($\bar{x}$ = 0.46, SD±0.23) compared to outdoors ($\bar{x}$ = 0.41, SD±0.18), the opposite was found for West *Sapajus* (indoor: $\bar{x}$ = 0.39, SD±0.20; outdoor: $\bar{x}$ = 0.43, SD±0.18). Overall, it would seem that both *Sapajus* groups are heterogeneous with respect to their individual activity budgets and as such could be considered asynchronous (Figure 5.3 A). The West and East *Saimiri* (see Figure 5.3B) were found to be more behaviourally synchronised when observed in the outdoor enclosures (West: $\bar{x}$=0.77, SD±0.24; East: $\bar{x}$=0.55, SD±0.26) compared to their indoor enclosures (West: $\bar{x}$=0.55, SD±0.24; East: $\bar{x}$=0.42, SD±0.17).

Furthermore, the East *Saimiri* appeared to be most homogenous when observed inside the *Sapajus* indoor enclosures ($\bar{x}$ = 0.580, SD±0.358). This also appeared to be the case with the West *Saimiri* ($\bar{x}$ = 0.80, SD±0.28), however they were only observed inside the *Sapajus* indoor enclosure for three (out of a potential 90) scans, and as such it is not possible to make any reliable inferences. That being said, it was expected that *Saimiri* would be more behaviourally synchronised when in the *Sapajus* indoor enclosures due to the combination of spatial constraints of being indoors, and group properties such as smaller group sizes and potential presence of *Sapajus* (which may indicate social monitoring – prediction 7.2). Upon examining the East *Saimiri* data more closely, *Saimiri* were found to be more synchronised in the *Sapajus* indoor enclosure when there were more *Sapajus* present ($\bar{x}$=0.81, SD±0.33) than when there were more *Saimiri* ($\bar{x}$=0.66, SD±0.37), however this difference was not significant (Shapiro Wilk tests, p<0.001; W=147.5, p=0.371).

Levene's tests found significant differences between the variability in behavioural synchrony scores for the collected data and the randomly generated data (based on individuals acting independently) for *Sapajus* (Levene's test = 10.38, p<0.01), *Saimiri* (Levene's test = 9.01, p<0.01) and mixed-species (Levene's test = 10.98, p<0.01). Mann-Whitney *U* tests identified a higher level of behavioural synchrony in the real samples compared to the randomly generated samples for *Sapajus* (real: $\bar{x}$ = 0.41, SD±=0.19; random: $\bar{x}$ = 0.31, SD±=0.14; W=21324, p<0.0001), *Saimiri* (real: $\bar{x}$ = 0.54, SD±=0.27; random: $\bar{x}$ = 0.40, SD±=0.23; W=24897, p<0.0001) and for mixed-species (real: $\bar{x}$ = 0.44, SD±=0.20; random: $\bar{x}$ = 0.34, SD±=0.11; W=6904, p<0.0001). I then proceeded to investigate which variables (see Table 5.2) might be contributing to behavioural synchrony using linear models (LM) and linear mixed models (LMM), before proceeding with running the full models using the 'Enter' method.

Due to group differences observed between *Sapajus* groups in their use of enclosure spaces (see Chapter 4), I wanted to explicitly examine group as a fixed effect rather than as a random factor in an LMM, which is why LMs were used. The results for *Sapajus* single-species LMs found no significant (p>0.05) contributing variables to behavioural synchrony, apart from a positive relationship with proportion males ($F_{1,255}$=4.852, p=0.018), and as such a full linear model was not attempted. However, an LM looking at the interaction between group and location was still examined due to the known differences in enclosure use between groups (see Chapter 4). The result was non-significant (p=0.091, see Table 5.4), but it is still worth noting that the interaction indicates a difference in the differences between groups; the West *Sapajus* were less synchronised in their indoor enclosure compared to outdoors, with the opposite finding for the East *Sapajus* (see Table 5.4 and Figure 5.3A).

Table 5.4 *Summary of linear models (LM) specifically examining the interaction between group and location on* Sapajus *(single-species scans) behavioural synchrony.*

Predictor Variables	**Estimate**	**SE**	***t***	***p***
***Sapajus* single-species** ($F_{3,253}$=1.092, p=0.3529)				
Intercept (location = indoor, group = East)	0.460	0.036	12.634	<0.0001
Group West (when location = indoor)	-0.072	0.043	-1.692	0.091
Location outdoor (when group = East)	-0.049	0.042	-1.174	0.242
Group*Location	0.087	0.053	1.653	0.099

For the single-species *Saimiri* an LM looking at the influence of group identified that behavioural synchrony was higher in the West *Saimiri* group compared to the East (LM: $F_{1,265}$=8.736, p=0.003), which may be attributed to the difference in the number of individuals in the West (N=9) and East (N=17) *Saimiri* groups. Therefore, in order to examine overall *Saimiri* behavioural synchrony I controlled for between group variability by including group as a random effect in the linear mixed models (LMM). An LMM examining the influence of the proportion of adults present in a scan identified a significant decrease in group synchrony as the proportion of adults in a scan increased (LMM:

$F_{1,265}$=12.095, *p*=0.001), similarly when looking solely at the influence of group size a negative relationship was identified between group size and behavioural synchrony (LMM: $F_{1,265}$=7.298, *p*=0.007). However, when looking at the impact of group size in the full model (see Table 5.5) it is no longer a significant contributor to group synchrony.

An LMM examining the influence of location identified a significant difference in behavioural synchrony when compared with a null model ($F_{2,264}$=11.637, *p*<0.0001). Post-hoc pairwise comparisons using the Bonferroni correction indicated that mean synchrony was significantly higher when *Saimiri* were in the *Sapajus* indoor enclosure ($\bar{x}$=0.66, SE=0.09) compared to their own indoor enclosures ($\bar{x}$=0.49, SE=0.08; *t*=3.340, *p*=0.003), synchrony was also higher in the outdoor enclosure ($\bar{x}$=0.64, SE=0.08) compared to when they were observed in their own indoor enclosure (*t*=-4.221, *p*=0.0001). No significant differences were found between group synchrony scores in the *Sapajus* indoor enclosure and outdoor enclosure. Weather and outdoor temperature did not contribute to behavioural synchrony, and as such were not included into the full model (see Table 5.5).

Table 5.5 *Linear mixed model (LMM) outlining contributing factors (predictor variables) to the* Saimiri *groups' behavioural synchrony, controlling for the imbalance in the number of individuals in the West (N=9) and East (N=17) groups (random factor), based on 180 scan observations of the two groups.*

Random factor	**Variance**	**SD±**		
Group (West/East)	0.00497	0.0705		
Predictor variables	**Estimate**	**SE**	***t***	***P***
Intercept (Location = *Sapajus* indoor)	0.801	0.089	9.027	<0.0001
Location (*Saimiri* indoor)	-0.152	0.057	-2.665	0.008
Location (outdoor)	-0.027	0.054	-0.510	0.610
Proportion adults	-0.240	0.091	-2.629	0.009
Group size	-0.004	0.006	-0.663	0.508
Full model $F_{4,233}$=7.589, *p*<0.0001				

In order to examine overall mixed-species behavioural synchrony I controlled for between group variability by including group as a random effect, however due to the small number of observations in the West *Sapajus* indoor enclosures (*N*=3) compared to the East (*N*=43), the resulting model produced a singular fit (explaining ~0% of the variance), and group was removed as a random effect. Therefore, I proceeded to use LMs without controlling for group. When examining the influence of the proportion of capuchins present in a scan on behavioural synchrony, a higher proportion of capuchins resulted in a marginal decrease in synchrony (LM: $F_{1,142}$=2.579, p=0.110). An LM examining the influence of location also identified a marginal decrease in synchrony when observed outside (LM: $F_{1,142}$=2.661, p=0.105), and an LM looking solely at the influence of group size identified a significant negative relationship between group size and behavioural synchrony (LM: *F*1,142=6.850, p=0.009). Having only found group size to be a significantly contributing factor to mixed-species behavioural synchrony, no further models were tested. However, it is worth examining whether there is an interaction between proportion *Sapajus* and location, given that there is some indication that *Saimiri* are behaving more synchronised when there is a higher proportion of *Sapajus* present (particularly in the East *Sapajus* indoor enclosure). An LM identified a significant interaction between location and proportion *Sapajus*, where behavioural synchrony significantly decreases in the outdoor enclosure compared to the indoor enclosure (see Table 5.6), which further indicates that *Saimiri* may be engaging in social monitoring behaviours towards *Sapajus* (prediction 7.2).

Table 5.6 *Summary of linear model (LM) specifically examining the interaction between proportion* Sapajus *and location on mixed-species behavioural synchrony.*

Predictor Variables	**Estimate**	**SE**	***t***	***p***
Mixed-species ($F_{3,140}$=2.537, p=0.059)				
Intercept (location = *Sapajus* indoor, when proportion *Sapajus* = 0)	0.434	0.07084	6.133	<0.0001
Proportion *Sapajus* (when location = outdoor)	0.083	0.12681	0.655	0.513
Location (outdoor)	0.238	0.14051	1.694	0.0924
Proportion *Sapajus**Location	-0.415	0.20187	-2.056	0.0416

When looking at the dataset as a whole (single-species and mixed-species), an LM examining the influence of group composition (i.e. just *Sapajus*, just *Saimiri* or mixed) on behavioural synchrony identified a significant difference when compared with a null model ($F_{2,665}$=20.270, p<0.0001). Post-hoc pairwise comparisons using the Bonferroni correction indicated that mean synchrony was significantly higher in the *Saimiri* single-species dataset ($\bar{x}$ =0.53, SE=0.01) compared to mixed-species ($\bar{x}$ =0.44, SE=0.02; t = -4.120, p=0.0001) and *Sapajus* single-species ($\bar{x}$ =0.41, SE=0.01; t = 6.126, p<0.0001). Therefore, while single-species *Saimiri* are meeting criteria for grouping (i.e. prerequisite 3), mixed-species groups are not. No significant difference was found between mixed-species and *Sapajus* single-species. An LM examining the influence of group size identified a significant negative relationship between group size and behavioural synchrony (LM: $F_{1,666}$=33.860, p<0.0001 – see Table 5.7 for the full model).

Table 5.7 *Linear model outlining significant contributing variables to behavioural synchrony for combined single-species and mixed-species data, based on 180 scan observations of the West and East groups.*

Predictor variables	**Estimate**	**SE**	***t***	***p***
Species type + Group size ($F_{3,664}$=18.48, p<0.0001)				
Mixed-species	0.537	0.032	16.617	<0.0001
Sapajus single-species	-0.048	0.024	1.677	0.094
Saimiri single-species	0.045	0.027	-2.011	0.045
Group size	-0.007	0.002	-3.754	<0.0001

In addition to comparing single-species scans with mixed-species scans, I wanted to examine how the mixed-species synchrony scans compared to what may be expected when taking the average scores of combined data (i.e. the average *Sapajus* and *Saimiri* scores) where both species were present in a scan. An LMM controlling for scan number (group was removed as a random factor in the model as it produced a singular fit explaining approx. ~0% of the variance), found that behavioural synchrony scores in the observed mixed-species scans were significantly lower compared to expected mixed-species synchrony scores (see Table 5.8).

Table 5.8 *Linear mixed model comparing observed and expected behavioural synchrony in the mixed-species groups, controlling for scan number (random factor), based on 75 scans (West=15; East=60) out of a possible 180.*

Random factor	**Variance**	**SD±**		
Scan number	0.0161	0.127		
Predictor variables	**Estimate**	**SE**	***t***	***p***
Intercept (mixed observed)	0.416	0.018	22.915	<0.0001
Mixed expected	0.048	0.012	4.047	<0.001
Full model $F_{1,85}$=16.377, p<0.001				

Correlations (using Kendall's tau) were used to test the relationship between behavioural synchrony scores and the frequency of monkeys performing each behaviour in the West and East groups. Vigilance was the only behaviour whose frequency in a scan was significantly correlated with behavioural synchrony across all groups (see Table 5.9; 5.10; 5.11): *Sapajus* (East: r_t= 0.314, p<0.0001; West: r_t= 0.281, p<0.0001), *Saimiri* (East: r_t= 0.358, p<0.0001; West: r_t= 0.297, p<0.0001) and mixed-species (East: r_t= 0.250, p=0.001; West: r_t= 0.501, p=0.002). This result is not unexpected, given the high proportion of vigilance across groups (see Figure 5.2). Rest was also found to be positively correlated with behavioural synchrony but only for the East *Saimiri* group (r_t= 0.233, p=0.03). Vigilant behaviour was found to be negatively correlated with foraging for East *Sapajus* (r_t= -0.217, p=0.005), and West *Saimiri* (r_t= -0.308, p=0.008). Vigilance was also negatively correlated with resting behaviour for both West *Sapajus* (r_t= -0.263, p=0.046) albeit with marginal significance, and West *Saimiri* (r_t= -0.372, p=0.020). While foraging was negatively correlated with locomoting (West *Sapajus*: r_t= -0.324, p=0.003).

Table 5.9 *Correlation matrix examining relationships between frequency of monkeys performing each behaviour and behavioural synchrony (BS) in West and East* Sapajus*, based upon 180 scan observations (90 scans per group); strongest positive correlations indicate behaviours that contributed the most to BS measures. Collinearity between behaviours were also examined. Kendall's tau statistic is presented with corresponding level of significance.*

	BS	**vigilant**	**forage**	**rest**	**locomote**	**groom**	**play**
East *Sapajus*							
BS	1	0.314***	-0.012	0.128	-0.160	-0.251	-0.140
vigilant	---	1	-0.217**	0.125	0.117	-0.125	-0.051
forage	---	---	1	-0.283	-0.068	-0.270	-0.149
rest	---	---	---	1	-0.131	-0.333	-0.096
locomote	---	---	---	---	1	-0.102	0.013
groom	---	---	---	---	---	1	-0.007
play	---	---	---	---	---	---	1
West *Sapajus*							
BS	1	0.281***	0.116	0.051	-0.113	0.055	-0.048
vigilant	---	1	0.070	-0.263*	-0.020	0.076	-0.052
forage	---	---	1	-0.397	-0.324**	0.462	-0.027
rest	---	---	---	1	0.064	-0.072	0.816
locomote	---	---	---	---	1	0.006	-0.027
groom	---	---	---	---	---	1	-0.005
play	---	---	---	---	---	---	1

$^*p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$

Table 5.10 *Correlation matrix examining relationships between frequency of monkeys performing each behaviour and behavioural synchrony (BS) in West and East* Saimiri, *based upon 180 scan observations (90 scans per group); strongest positive correlations indicate behaviours that contributed the most to BS measures. Collinearity between behaviours were also examined. Kendall's tau statistic is presented with corresponding level of significance.*

	BS	**vigilant**	**forage**	**rest**	**locomote**
East *Saimiri*					
BS	1	0.358***	-0.036	0.233*	-0.110
vigilant	---	1	-0.053	0.004	-0.036
forage	---	---	1	-0.208	0.008
rest	---	---	---	1	0.179
locomote	---	---	---	---	1
West *Saimiri*					
BS	1	0.297***	-0.063	0.249	-0.223
vigilant	---	1	-0.308**	-0.372*	-0.039
forage	---	---	1	-0.378	-0.132
rest	---	---	---	1	0.290
locomote	---	---	---	---	1

$^*p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$

Table 5.11 *Correlation matrix examining relationships between frequency of monkeys performing each behaviour and behavioural synchrony (BS) in West and East mixed-species groups, based upon 180 scan observations (90 scans per group); strongest positive correlations indicate behaviours that contributed the most to BS measures. Collinearity between behaviours were also examined. Kendall's tau statistic is presented with corresponding level of significance.*

	BS	**vigilant**	**forage**	**rest**	**locomote**	**play**
East mixed-species						
BS	1	0.250***	0.026	-0.007	-0.156	-0.207
vigilant	---	1	0.045	0.210	0.176	0.0.26
forage	---	---	1	-0.077	0.108	-0.191
rest	---	---	---	1	-0.061	-0.224
locomote	---	---	---	---	1	-0.208
play	---	---	---	---	---	1
West mixed-species						
BS	1	0.288**	-0.078	0.013	-0.621	0.275
vigilant	---	1	-0.024	-0.816	-0.483	0.163
forage	---	---	1	-0.830	-0.301	-0.406
rest	---	---	---	1	0.091	-0.816
locomote	---	---	---	---	1	-0.490
play	---	---	---	---	---	1

*$p<0.05$, **$p<0.01$, ***$p<0.001$

Table 5.12 *Spearman correlation coefficients examining the relationship between age class, sex and group size with the proportion of behaviours in East and West* Sapajus.

	vigilant	**forage**	**rest**	**locomote**	**groom**	**play**
East *Sapajus*						
proportion adult	-0.236*	-0.001	0.057	0.152	-0.014	-0.049
proportion male	-0.051	-0.113	-0.072	0.030	-0.018	-0.010
group size	0.248**	0.014	0.117	-0.165	0.052	0.161
West *Sapajus*						
proportion adult	0.019	0.118	0.064	0.053	0.071	0.007
proportion male	0.149	0.154	0.941	0.150	0.077	-0.013
group size	-0.240**	-0.409***	0.097	-0.204**	0.200**	-0.165*

*$p<0.05$, **$p<0.01$, ***$p<0.001$

Table 5.13 *Spearman correlation coefficients examining the relationship between age class, and group size with the proportion of behaviours in East and West* Saimiri. *Sex was excluded due to both groups only containing one male.*

	vigilant	**forage**	**rest**	**locomote**
East *Saimiri*				
proportion adult	-0.127	-0.105	0.116	0.201
group size	-0.172*	0.037	0.308***	0.143
West *Saimiri*				
proportion adult	-0.127	0.083	0.046	0.153
group size	-0.263**	0.114	0.425***	0.080

*p<0.05, **p<0.01, ***p<0.001

Table 5.14 *Spearman correlation coefficients examining the relationship between age class, species and group size with the frequency of behaviours in East and West mixed-species groups. Sex was excluded due to both* Saimiri *groups only containing one male, rest was excluded from the West mixed-species analysis due to insufficient data (n=3).*

	vigilant	**forage**	**rest**	**locomote**
East mixed-species				
proportion *Sapajus*	-0.141	0.202*	0.0.48	-0.052
proportion adult	0.190*	-0.287**	0.070	-0.133
group size	-0.146	0.157	0.120	0.225*
West mixed-species				
proportion *Sapajus*	-0.161	0.262	-0.078	0.154
proportion adult	-0.067	0.140	0.176	0.082
group size	-0.005	0.016	0.008	0.091

*p<0.05, **p<0.01, ***p<0.001

For each behaviour, the correlation between the proportion of adults and group size was examined for West and East *Sapajus* and *Saimiri* groups (see Table 5.12; 5.13), and proportion of *Sapajus* for mixed-species groups (Table 5.14). A negative relationship was identified between the proportion of adult monkeys observed in a scan and vigilant behaviour in the East groups (*Sapajus*: r_s= -0.349, p<0.001; *Saimiri*: r_s= -0.2.05, p=0.01; mixed-species: r_s= -0.319, p<0.01). This was not found for the West groups, though the proportion of males present during a scan negatively correlated with the frequency of vigilant behaviour (r_s= -0.259, p<0.01). Play was also identified as having a significant relationship with the proportion of adults present (Table 5.12), though the direction varied between the groups; negative for West *Sapajus* (r_s= -0.342, p=0.020) and positive for East *Sapajus* (r_s= 0.328, p= 0.050). Foraging was only found to be negatively correlated for East mixed-species (r_s= 0.321, p<0.01).

A positive relationship was identified between group size and the frequency of vigilant behaviour observed during scans for *Sapajus* (see Table 5.12), *Saimiri* (see Table 5.13) and mixed-species (see Table 5.14). Similar relationships were identified for foraging, resting and locomoting in the West *Sapajus* (grooming only for *Sapajus*) and *Saimiri* groups, though not for West mixed-species. Group size was also positively correlated with foraging and locomoting for East mixed-species (see Table 5.14). The proportion of *Sapajus* present in mixed-species scans was found to have a positive correlation with the frequency of vigilant behaviour observed in both the West (r_s= 0.664, p<0.001) and East (r_s= 0.815, p<0.001) mixed-species groups. Foraging was also found to correlate with proportion of *Sapajus* present, but only for the East mixed-species group (r_s= 0.321, p<0.01).

5.5 Discussion

When observing two animals, they will either behave in the same way or not. The expectation that the same behaviour will occur in both individuals at the same point is simply based on the relative behavioural frequencies and durations of behaviours in the two partners (Lamprecht, 1985). However, when there are more than two individuals involved then attempting to determine the extent of behavioural synchrony becomes more difficult, due to the fact that while an individual may be behaving in synchrony with some members of its group, it will be asynchronous with others. I adopted an approach based on King and Cowlishaw's (2009) study to investigate overall behavioural synchrony across all observable group members. To my knowledge this is the first study to examine behavioural synchrony at the group level in mixed-species groups of Neotropical primates in a captive environment. The degree of behavioural synchrony in the two mixed-species groups of captive *Sapajus* and *Saimiri* was significantly greater than expected based on a randomly generated dataset where individuals behaved independently of each other.

The predictions were based on three overarching concepts (e.g. activity budgets, spatial constraints, and group properties), which are each considered in turn. It was predicted that there would be a decrease in mixed-species behavioural synchrony compared to single-species, based on the phenotypic differences between *Sapajus* and *Saimiri* (prediction 1.1), which was supported by the findings for *Saimiri* (see Table 5.6), but not for *Sapajus*, though the difference was only marginally significant (p=0.094). This could be attributed to the overall higher proportion of capuchins present in shared enclosures (see Table 5.3), and the generally lower frequency of observations where the West *Saimiri* were in shared enclosures. The findings do suggest that the monkeys are behaving asynchronously, which complements previous literature relating to phenotypic differences in energy requirements (Bell, 1971; Geist, 1974; Fleagle & Mittermeier, 1980; Demment & van Soest, 1985; Kamilar & Pokempner, 2008), but contradicts mixed-species studies in the wild where *Sapajus* and *Saimiri* have been observed foraging and travelling together (e.g. Fleagle et al., 1981; Terborgh, 1983; Podolsky, 1990).

Contrary to prediction 2 the proportion of adults present in a scan (within-species phenotypic variation) was not found to contribute to *Sapajus* behavioural synchrony, and a negative relationship was found for *Saimiri* (see Table 5.5). When further examining the relationship between the proportion of adults present during scans and the frequency of play behaviours (see Table 5.2) observed, no significant correlations were found for the West or East *Sapajus*, (play was not examined in *Saimiri* due to the low frequency of the behaviour). Possible explanations for the low frequency of observed play could be due to individual differences, such as non-reciprocation of intended play partner(s), or due to adults also engaging in play behaviours and differences in group dynamics. Further correlations identified that the proportion of adults present had a significantly negative relationship with vigilance in the East *Sapajus* (see Tables 5.12, 5.13, 5.14), which is contradictory to literature suggesting that younger individuals are at greater risk of predation than adults, and as a result show higher rates of vigilance than adults (e.g. Alberts, 1994; Mateo, 1996; Hanson & Coss, 2001). However, other studies have reported the opposite (e.g. Fragaszy, 1990; Arenz & Leger, 2000; Boinski et al., 2003; Gosselin-Ildari & Koenig, 2012), postulating that this is due to age-specific differences in an animal's requirements, for instance juveniles are more likely to engage in other behaviours such as play and have higher nutritional and feeding requirements that may compete with anti-predator behaviours such as vigilance. This is particularly likely to be the case in captivity, where there are minimal threats of predation. Phenotypic differences in relation to sex (*Sapajus* only) found a significant positive relationship between behavioural synchrony and the proportion of males present in a scan, which is the opposite of what I expected to find (prediction 3). This finding could be attributed to the captive environment, whereby males are less likely to incur the same energy costs as they would in the wild (e.g. Leutenegger & Kelly, 1977; Kenagy & Trombulak, 1986; Dietz, Baker & Miglioretti, 1993; Alberts et al., 1996; Melfi & Feistner, 2002), and as such can dedicate more time to other activities such as foraging and resting. However, the overall rate of foraging and resting between males and females was very low in comparison to the rate of vigilance (approx. 0.50), which made up the majority of *Sapajus* activity budgets (see Figure 5.2A). Overall, the data did not provide sufficient support for phenotypic differences (sex-age class) as contributors to single-species or mixed-species group synchrony in relation to the activity budgets hypothesis [H1].

There were mixed findings relating to the habitat/spatial constraints hypothesis [H2], and predictions related to location (predictions 4 & 5). Mean behavioural synchrony was found to be <0.50 for both the West and East *Sapajus* groups irrespective of location (Figure 5.3A), and an LM confirmed that location was not a significant contributor to behavioural synchrony. However, when considering the interaction between location and group (East/West), it was clear that there were differences between groups. East *Sapajus* were more synchronous in their indoor enclosure compared to when they were outdoors (complementing previous findings, e.g. Couzin & Krause, 2003; Braune et al., 2005; Cortopassi & Bradbury, 2006; Couzin, 2009; King & Cowlishaw, 2009; Sumpter, 2010), whereas the opposite was found for the West group (see Table 5.4). Given that there are less spatial constraints in the outdoor enclosure (outdoor enclosure: 900m^2, *Sapajus* indoor: 7m x4.5m x 6m), and the average distance between conspecifics is likely to be greater when in the outdoor enclosure, we might expect behavioural synchrony to be lower in the outdoor enclosure, as long as the monkeys were making use of all of the available space. The findings in Chapter 4 indicate that while *Sapajus* were observed utilising most zones in their outdoor enclosures, there was a higher rate of observations in the central tree area. This in itself (as noted in Chapter 4 Section 4.6) could be acting as a spatial constraint and may explain why behavioural synchrony was slightly higher in the outdoor enclosure for the West group. But then why was this not also found in the East *Sapajus* group? Perhaps this effect could be attributed to increased heterogeneity with regard to hierarchical composition when in an enclosed space. For instance, monkeys of varying social status may interpret their enclosed environment differently, with higher ranking individuals possibly perceiving their indoor environment as a safe space in which they can rest. However, the perceived threat of aggression from higher ranking individuals may increase more vigilant behaviours in subordinate individuals. Therefore, even though the West monkeys may be using specific areas of their outdoor enclosure, there is still sufficient space (both vertical and horizontal) for subordinate monkeys to retreat, and as such the perceived risk of aggression may be lower in the outdoor enclosure allowing for more synchronous behaviours (e.g. foraging) to occur. There could be other reasons for this interaction between group and location, however it is still important to consider the possibility that environmental, in conjunction with social cues may be interpreted and acted upon in different ways by different individuals, and as a result will generate behavioural diversity within a group.

Based on previous findings (e.g. Boinski et al., 2003; King & Cowlishaw, 2009 – see also Chapter 4), it was predicted that *Saimiri* behavioural synchrony would be consistent irrespective of enclosure (prediction 4), however this was only noted when the monkeys were in shared enclosures (outdoor and *Sapajus* indoor). Additionally, the proportion of vigilant behaviours was found to be higher for both *Saimiri* groups when they were in the outdoor enclosure and for the East group when they were observed in the *Sapajus* indoor enclosure (too few data in the West group to test), compared to their own indoor enclosures (see Figure 5.2B). It is important to note that single-species data was taken from mixed-species scans, meaning that the presence of one species could have been impacting on the behaviour of the other. This may explain why these findings indicate that *Saimiri* were more behaviourally synchronised in single-species scans when compared with mixed-species scans (see Table 5.7). Furthermore, given the high proportion of vigilance observed (Figure 5.2 B) in *Saimiri* the results of the LMs could be indicating that *Saimiri* were engaging in social monitoring of the larger more dominant *Sapajus*.

In relation to variability in synchrony due to group properties [H3], I predicted (predictions 6, 7, 8.2) that if the monkeys were performing social monitoring behaviours towards more dominant individuals within or between species, then behavioural synchrony would decrease with group size. The results relating to location and activity budgets (high proportion of vigilant behaviours, see Figure 5.2A) indicate that *Sapajus* may be engaging in social monitoring, and therefore it was expected that group size may also be a contributing factor to behavioural synchrony, but this was not reflected in the results ($p>0.05$). However, for *Saimiri* and mixed-species groups, behavioural synchrony was found to significantly decrease in larger groups. When examining the relationship between group size and the frequency of other observed behaviours (see Tables 5.13, 5.14, 5.15) it was found to positively correlate with foraging, which complements previous research that larger groups better facilitate foraging (e.g. de Ruiter, 1986; Ebensperger et al., 2006; Beauchamp, 2006; Pays et al., 2009). Likewise, group size was positively correlated with vigilance, and while this does complement previous findings suggesting that heightened vigilance in larger groups is due to the pressure of monitoring conspecifics or heterospecifics (e.g. Caine & Marra, 1988; Hirsch, 2002 – see also Chapter 4), generally increased foraging due to larger group size would result in reduced vigilance (e.g. Cody, 1971; Hamilton, 1971; Krebs et al., 1972; Treisman, 1975a, 1975b; Pulliam, 1976; Bertram, 1978; Kenward, 1978; Elgar, 1989; Lima & Zollner, 1996 – see also Chapter 1), but perhaps this may be due to larger groups typically engaging more frequently in these two behaviours. When examining the correlation between vigilance and foraging, a negative relationship was found, but only for East *Sapajus* (see Table 5.10) and West *Saimiri* (see Table 5.11).

Finally, it was expected that ecological conditions such as weather, time of day and outdoor temperature would be a contributing factor to behavioural synchrony (prediction 9), as previous research found differences in activity budgets and enclosure use (i.e. outdoors more when ≥32ºC) based on these factors (e.g. Ross & Giller, 1988; O'Neill, 1994; Suichi & Rothe, 1999; Goodenough et al., 2019), however, none were found to contribute to behavioural synchrony ($p>0.05$). Despite this finding it is still important to consider these ecological factors in future research, especially as the data were limited to zoo opening hours during the summer months, leaving approximately 16 hours of the day and nine months of the year unaccounted for. Being in the northern hemisphere, Edinburgh will have longer days during the summer months, and shorter in the winter months, with a variety of weather conditions and temperatures (<5ºC - >20ºC, Met Office), and as such it is likely that long-term data collection over the 24-hour period will find differences in the rates of behavioural synchrony. Animals are less likely to spend time in outdoor exhibits during inclement weather or if temperatures are too cold (Brando & Buchanan-Smith, 2018). Ecological factors will vary from day, night, week, year, and seasons, and it would be imprudent to think that this does not impact behaviour.

It is important to note that the single-species data reported were not truly based on single-species scans, as both species could have been present regardless. This means that in those enclosures where both species were able to gain access (i.e. *Sapajus* indoor enclosures and outdoor enclosures) the presence of one species could have been impacting on the behaviour of the other. Moreover, not all individuals were sampled for all scans as they were out of sight of the observer. Therefore, in order to make more direct comparisons between single-species and mixed-species group synchrony it will be necessary to control for this in future research. Likewise, it may be argued that because of the scanning procedure, the behaviours documented may not be exactly synchronized. Some behaviours may have lasted longer than others during a scan, and although scanning was done in the fastest method possible to cover the entire exhibit (outdoor enclosure, *Sapajus* indoor and *Saimiri* indoor), while still being able to view as many monkeys as possible, some behaviours might have changed or been missed. A ‘snapshot’ photo would provide an actual synchronous scan, but this presents its own issues, for instance it would be difficult to differentiate between moving behaviours, or identifying individuals not facing the camera. Also due to the dimensions and number of enclosures within the exhibit, multiple photos would be needed, which would also remove precise synchrony at the point of sampling. Perhaps in future studies focal follows in conjunction with group scans could be adopted.

Overall, this chapter has summarised and examined how behavioural synchrony can be affected by variations in activity budgets [H1] across individuals between and within species, location [H2] and group properties [H3]. Observations of the monkeys during the study indicate that they were not behaviourally coordinated in time and space (i.e. prerequisite 3) as one synchronous mixed-species group, but rather as two single-species groups sharing an exhibit. This corroborates the findings in Chapter 4, with the monkeys using different areas of their shared outdoor enclosures (*Sapajus* central areas, *Saimiri* on the periphery). Part of the husbandry of maintaining animals in a mixed-species exhibit should be ascertaining their social relationships, as this knowledge can help guide their care. It is therefore necessary to take both environmental and social relationships into consideration in exhibit design (e.g. Nuttall, 2004; Leonardi et al., 2010; Buchanan-Smith et al., 2013; Brando & Buchanan-Smith, 2018).

The mechanism of behavioural synchrony is achieved on the level of the individual, but as mentioned earlier in this section, while an individual may be engaged in the same activity with some group members at a particular point in time, it may be asynchronous with others. Furthermore, group level synchrony does not take into consideration the possibility of the influence of subgroups, or of a particular species (if considering mixed-species) on behavioural synchrony. Thus, a study that investigates the interaction between group level and individual level effects will introduce exciting possibilities for future directions of animal behaviour research. One way that this could be achieved is to assess the degree of synchrony of a specific individual (focal) with respect to other group members (e.g. Engel & Lamprecht, 1997). While the focus of this chapter has been group-level behavioural dynamics, the next will focus on individual relationships in single-species and mixed-species groups in relation to prerequisites 1 and 2 (see Chapter 1, Section 1.1) using social network analyses.

6 SOCIAL NETWORKS IN A MIXED-SPECIES EXHIBIT

6.1 Abstract

Mixed-species groups have been recorded in a number of different primate species, including *Sapajus* and *Saimiri*. However, measures of their 'groupness' are generally based on duration (i.e. stability), attraction (i.e. not present due to aggregating around a resource) and distance (within <20-50m – see Chapter 1). In recent years social network analysis (SNA) has become a useful tool in the field of animal behaviour for quantifying relationships between individuals in a group based on proximity and specific behaviours (e.g. grooming or aggression). In this chapter I apply SNA's to compare *Sapajus* and *Saimiri* single-species and mixed-species groups, with the aim of examining their stability and socialness (prerequisites 1 & 2 respectively). Network parameters were based on proximity data (≤40cm - distance determined as the body length of the largest monkey) as a proxy measure for interactions. Three network measures were applied: eigenvector centrality, density, and clustering coefficients. Overall, network density was found to be sparse across all types of groups, while eigenvector centrality was strongly affected by species (*Sapajus* were more central than *Saimiri*) and network diagrams for both mixed-species groups showed distinct clusters separating *Sapajus* and *Saimiri*. Clustering coefficients indicate key individuals who may be strong contributors to group stability. There were also distinct differences between the Living Links East and West groups suggesting factors such as dominance hierarchies, relatedness and individual differences may be affecting association patterns. Stability of

Sapajus and *Saimiri* single-species networks did not vary greatly between mixed-species networks, however few and weak ties between species indicate that frequency of interactions (i.e. came into proximity in time and space) were low, indicating that they were not behaving as true mixed-species groups.

6.2 Introduction

A key feature of animal groups is that there is 'an element of socialness' (see Chapter 1, Section 1.1.), implying that individuals living and/or interacting together can lead to complex social relationships and structure (i.e. group stability). However, the ability to quantify social structure and the mechanisms and functions that underpin it has long been a challenge within the areas of psychology, ethology, ecology and evolutionary biology; especially when considering the link between individual and group behaviour (Thorpe & Zangwill, 1961; Hinde, 1966, 1976; Tinbergen, 1974; Barnard, 1983; Lima & Zollner, 1996; Sutherland, 1996; Whitehead, 1997, 2008; Croft, James & Krause, 2008; Croft, Madden, Franks & James, 2011). Behaviour has been described as an individual's response to both intrinsic and extrinsic factors, including their physical and social environment(s) (e.g. Hinde 1966, 1976; Tinbergen, 1974). The social environment includes direct (e.g. physical contact) and indirect (e.g. proximity, observation) interactions with other individuals (Hinde 1966, 1976; Alexander, 1974; Tinbergen, 1974; Krause & Ruxton, 2002; Croft et al., 2008). Consequently, an individual's interactions with their social and/or physical environment will have an impact on their ability to access information and resources. This in turn will have implications for key 'survival' behaviours, including: locating and selecting a sexual partner, the development and maintenance of cooperative relationships, and engaging in foraging and anti-predator behaviours (Marler & Hamilton, 1966; Hinde, 1966; Alexander, 1974; Tinbergen, 1974; Lee, 1994; Croft et al., 2008; Wey, Blumstein, Shen & Jordan, 2008; Sih, Hanser & McHugh, 2009 – see also Chapter 1). Likewise, such behaviour and the resulting local and global population structures that are produced have implications for population patterns and processes (i.e. habitat use, disease transmission, information flow, and mating systems), which in turn form the basis for evolutionary processes including adapting to changing environments, sexual selection, and speciation (Alexander, 1974; Tinbergen, 1974; Harvey, 1994; Croft et al., 2008; Wey et al., 2008; Sih et al., 2009; Croft et al., 2011). It can be further argued that communicative and complex cognition is an important correlate and perhaps even an evolutionary determinant of social structure (Jolly, 1966; Alexander, 1974; Humphrey, 1976; Whiten & Byrne, 1988a; Lee, 1994; Byrne & Whiten, 1997). Thus, our understanding of the ultimate and proximal functions of social organisation will be enhanced by establishing why certain patterns of association develop and how inter-individual association patterns affect group- or population-level structures.

Patterns of association can arise as a result of individuals sharing identical or similar motivations and/or behaviours such as the degree to which they are hungry, thirsty or how they respond to a potential threat (e.g. Hinde, 1976, 1983a, 1983b; Lee 1994). Such association patterns can have the potential to reduce some of the costs of group-living, as group cohesion is easier to maintain when there are fewer conflicts of interest between individuals (Wrangham, 1983; Conradt & Roper, 2000; Ramos-Fernandez, Boyer, Aureli & Vick, 2006; King & Cowlishaw, 2009 - see also Chapter 5). However, circumstances in which sociality results in asymmetric payoffs (e.g. while larger groups reduce the risk of predation, they also lead to greater competition for resources), will require some form of buffer (e.g. grooming or vertical stratification) in order to stem the effects of competition and maintain group stability (de Waal, 1986; Janson & Goldsmith, 1995; Gould, 1997; Hardie & Buchanan-Smith, 1997; Hill & Lee, 1998; Stensland, Angerbjörn & Berggren, 2003; Clutton-Brock, 2009; Sueur, Jacobs, Amblard, Petit & King, 2011). In this context, variability in social structure can be understood in terms of an individual having to respond to their social and physical environments, which is perhaps why more traditional research in ethology has focussed predominantly on focal individuals, dyads, triads or has been restricted to statements about averaged behaviour at the group-level (e.g. Kummer, 1968, 1978; de Waal & Yoshihara, 1983; Hinde, 1983a, 1983b; Camazine et al., 2003; Couzin & Krause, 2003; Perry, Barrett & Manson, 2004).

Yet we know that social relationships and social structure are more complex than this. A variety of measures has been applied to the study of social complexity, such as: the presence of a linear dominance hierarchy (e.g. Holekamp, Sakai & Lundrigan, 2007; MacLean, Merritt & Brannon, 2008); fission-fusion dynamics (e.g. Couzin, 2006; Amici, Aureli & Call, 2008; Aureli et al., 2008); pair bonds (e.g. Shultz & Dunbar, 2007); complex alliances (e.g. Perry et al., 2004; Connor, 2007); tactical deception (e.g. Whiten & Byrne, 1988a, 1988b; Byrne & Corp, 2004) and group stability (e.g. Shultz & Dunbar, 2007) to name a few (for a review see Bergman & Beehner, 2015). Freeberg, Dunbar and Ord (2012, p. 1787) define social complexity as social systems in which "*individuals frequently interact in many* *different contexts with many different individuals, and often repeatedly interact with many of the same individuals over time*". Group-living animals will therefore engage in non-random (and in some instances complex) interactions that require individuals to develop behavioural strategies (Dunbar, 1989), resulting in the formation of a multi-layered and multi-behavioural structure (e.g. Hemelrijk, 1990a, 1990b; Whitehead, 2008; Sosa, 2016). Consequently, in order to better understand the complexity of a social structure, we need to consider the behaviour of individuals in relation to the dynamics of group-level properties (i.e. ideally analyse all relationships among all group members).

There is immense diversity in social behaviour throughout the animal kingdom, especially in socially complex species such as the non-human primates, with social interactions differing in type (e.g. cooperative, antagonistic, or sexual) as well as frequency and duration (e.g. years, days or minutes). Furthermore, the type of interactions that occur in addition to their frequency and duration, will likely depend on factors such as kinship, dominance, body size, sex, age, and general health (e.g. parasite load) of the participating individuals (e.g. Hinde, 1966, 1976; Alexander, 1974; Tinbergen, 1974; Marler & Hamilton, 1966; Lee, 1994; Hemelrijk, 2000; Croft et al., 2008; Sosa, 2016). Spatial proximity should also be considered, as individuals are not generally able to interact and/or react (e.g. cooperate, flee, gain information) if they are not close enough to other individuals (Perry, Manson, Muniz, Gros-Louis & Vigilant, 2008; Silk, Alberts & Altmann, 2004; Crofoot, Rubenstein, Maiya & Berger-Wolf, 2011; Zhang, Li, Qi, MacIntosh & Watanabe, 2012). Primatologists have used a variety of different measures to quantify aspects of social bonding behaviours, such as grooming patterns, social proximity, coalition formation and reconciliation (e.g. Cords, 1997; Perry et al., 2004; Lehmann, Korstjens & Dunbar, 2007; Lehmann & Ross, 2011; Tiddi, Aureli & Schino, 2011). Other examples may focus on social position based on hierarchical/dominance rank (usually calculated from frequencies of wins and losses during displacements or aggressive interactions – see Bernstein, 1981; Drews, 1993). However, it is not always easy to determine an individual's social position within a group when the hierarchy is non-linear (i.e. social position cannot be determined for all individuals) or when power is not linearly distributed (e.g. Boyd & Silk, 1983; Newton-Fisher, 2017).

Non-linear social systems are common for many group-living Neotropical monkeys (Jones, 1980; Kinzey & Cunningham, 1994; Strier, 1997), including all species of capuchins (*Cebus* spp. & *Sapajus* spp. - Fragaszy, Visalberghi & Fedigan, 2004; Rylands & Mittermeier, 2013 – see also Chapter 1). However, *Saimiri sciureus* are described as forming single linear dominance hierarchies (Boinski, 1999; Rylands & Mittermeier, 2013 – see also Chapter 1). While it is almost always possible to determine the alpha male (in *Sapajus* spp. and *Saimiri* spp.) and alpha female (*Sapajus* spp.), along with which individuals are subordinates (low ranking), it is not always possible to distinguish for instance the 3rd from the 4th ranking individuals and so on (Izawa, 1980; O'Brien 1991; Fedigan, 1993; Fragaszy et al., 2004). Furthermore, *Sapajus* spp. have generally been found to be quite tolerant towards "subordinate" others, including non-kin (Fragaszy et al., 2004; Ferreira, Izar & Lee, 2006) and other species (e.g. *Sapajus* spp. with both *Saimiri* spp. and *Chiropotes* sp. - see Fleagle & Mittermeier, 1981; Mittermeier & van Roosmalen, 1981; Terborgh, 1983; Podolsky, 1990; Levi et al., 2013), and compared to many Old World cercopithecines (e.g. rhesus macaques (*Macaca mulatta*) – Symons, 1978; de Waal & Ren, 198, and olive baboons (*Papio anubis*) – Packer & Pusey, 1979; MacCormick et al., 2012) both *Sapajus apella* and *Saimiri sciureus* exhibit relatively low rates of aggression (Boinski, 1990; Cooper et al., 2001; Fragaszy et al., 2004). Even in captivity both *Sapajus* spp. and *Saimiri* spp. are mostly able to manage competition and conflict with few cases of intra-specific aggression (Boinski, 1990; Fragaszy et al., 2004; Leonardi et al., 2010; Buchanan-Smith et al., 2013).

Additionally, the relaxed nature of the social relations in captive groups of *Sapajus* and *Saimiri* is evidenced in their spacing during feeding bouts, where one individual will commonly approach another to sit next to while eating (e.g. Fragaszy et al., 2004; personal observations, 2009; 2015). For these reasons, it can be quite challenging to determine social position, and even more so when considering mixed-species groups. Inclusive fitness can be excluded *a priori* for explaining mixed-species social relationships, making mixed-species sociality particularly important to our understanding of how direct fitness benefits (e.g. improved foraging and reduced risk of predation) can produce complex social structures in the absence of kinship. Two classic examples given to explain social behaviour among unrelated individuals of the same, or different species are (1) mutualism (e.g. Hamilton, 1964; Trivers 1972; Hemelrijk, 1994; Kokko et al., 2001; West, Griffin & Gardiner, 2007 – see review in Clutton-Brock, 2009) and (2) manipulation (e.g. de Waal, 1982; Terborgh, 1983; Whiten & Byrne, 1988a, 1988b; Hauser, 1992; Lee, 1994; Byrne & Whiten, 1997;

Dugatin, 1997– see review in Clutton-Brock, 2009). Mutualistic interactions are based on shared benefits, such as cooperative foraging and resource defence which exceed the costs associated with interacting. In contrast, with manipulative social behaviours, the benefits are likely to be disproportionate, with one species or individual benefiting more than the other.

There have been several methods devised to quantitatively measure social complexity (e.g. association matrices and multivariate methods – see Hemelrijk, 1990a, 1990b; Whitehead, 1997; Bejder, Fletcher & Bräger, 1998; Whitehead, 1999; Bayly, Evans & Taylor, 2006). Some studies have used composite indices of sociality, which combine several behavioural measures (that are often correlated) into one-dimension, and are then subsequently used for statistical analyses (Cords & Aureli, 1993; Drews, 1993; Whitehead, 1997, 1999; Silk, Alberts & Altmann, 2003; Fraser, Schino & Aureli, 2008). For instance, Silk et al. (2003) used a composite sociality index to investigate the effects of social bonding in adult female yellow baboons (*Papio cynocephalus*) on infant survival, combining data on proximity (within 5m) and grooming behaviour. While Fraser et al.'s (2008) study on a group of captive chimpanzees (*Pan troglodytes*) used principal components analysis to extract three key components of relationship quality based on nine different behaviours. However, the use of social indices and association matrices can suffer from several restrictions, for example the analytical approach can often be univariate, and so researchers will need to either make critical decisions about which measure to include in their measure of social connections by running separate analyses or, combine the different measures into one variable with loss of variance and assumption of underlying continuity (Whitehead, 1997; Fraser et al., 2008). The main issues here are that the resulting outputs are not entirely representative of the relationships among individuals and the group as a whole, which are key elements to understanding social structure and complexity.

Therefore, in order to better understand social structure and the link between the behaviour of individuals with group-level properties, we need to consider and analyse relationships that potentially link all group members (e.g. Hemelrijk, 1990a, 1990b; Croft et al., 2005; Whitehead, 2008; Sueur et al., 2011). While this is not a new concept (e.g. Hinde, 1976), it is often difficult to measure quantitatively. Therefore, our understanding can perhaps be considerably expanded by a shift in analytical focus. One approach is social network analysis (hereafter SNA), a method based on mathematical graph theory (e.g. Kummer, 1957, 1968; Sade, 1965, 1972; Wilson, 1975; Cheney, 1978a, 1978b; Hinde, 1983a, 1983b;

Whitehead, 1997, 1999, 2008, 2009; Scott, 2000, 2013) that examines social relationships within a wider context. For instance, social groups can be analysed by examining individual social behaviours not only within the context of their own direct relationships with others but also by their indirect relationships. Furthermore, central individuals have been found to be integral in maintaining social/group cohesion, have greater knowledge of their environment and tend to be high ranking (e.g. Lusseau & Newman, 2004; Kanngiesser, Sueur, Riedl, Grossmann & Call, 2011). Thus by gaining insights into the position and role of the individual within a group, it is possible to build a more complete picture of the complex sociality and structure of group-living animals (Wasserman & Fraust, 1994; Berman, Rasmussen & Suomi, 1997; Krause, Croft & James, 2007; Krause et al., 2009; Lehmann & Ross, 2011; Sueur et al., 2011; Boccaletti et al., 2014; Sosa, 2016).

SNAs are also able to produce diagrammatic representations of animal groups (Kummer, 1957, 1968; Sade, 1965, 1972; Wilson, 1975; Cheney, 1978a, 1978b; Hinde, 1983a, 1983b; Croft et al., 2008; Makagon, et al., 2012), which enables the visual identification of (1) key individuals that may be central to the cohesion of a specific group; (2) relationship preferences and the strength of these relationships; (3) which individuals link specific sub-groups together (e.g. Krause et al., 2009). Individuals within a social system are represented in a sociogram (or social network diagram) as ‘nodes’ and associations/interactions between individuals are shown by lines (‘edges’), whose thickness (‘weighting’) and direction are used to provide meaning to the connections within a group (e.g. Croft et al., 2008). The resulting network can provide a more complete picture of an individual’s social connections by quantifying how central an individual is (see Table 6.1 for definition of centrality measures), and to determine which individual properties (e.g. species, kinship, sex or age) can be used to predict position. For a zoological collection, such data can be useful in determining how positive welfare states can be maintained over the long term (Rose & Croft, 2015), or to monitor the impact of how a change in environment (e.g. move to new enclosure) can affect social networks (Dufour, Sueur, Whiten & Buchanan-Smith, 2011).

Table 6.1 *Glossary of network terminology used (adapted from Coleing, 2009).*

Network term	**Description**
Node	represents an individual within a network diagram (also known as vertex)
Tie	relationship between two nodes of the network (also known as edge or arc)
Node degree	the number of ties an individual has to others in the network
Association indices	**Description**
Clustering coefficient	measure of how well the associates of an individual are themselves associated.
Eigenvector centrality	measure of how well an individual is associated to other individuals that are also well associated.
Degree centrality	measure based on the number of arcs a vertex has; a higher value means an individual has more contacts, is more central to the network and therefore has more influence on the social network
Betweenness centrality	measure indicating how important an animal is as a point of social connection and transfer. A high value indicates that an individual is influential in the group

Previous studies on *Sapajus-Saimiri* mixed-species groups (wild and captive) have mostly focussed on the frequency/duration of associations, or compared the differences in activity budgets when in single-species or mixed-species observations (Klein & Klein, 1973; Terborgh, 1983; Whitesides, 1989; Podolsky, 1990; Leonardi et al., 2010; Buchanan-Smith et al., 2013 – see also Chapter 2). Furthermore, measures of association were limited to arbitrary distances between individuals of the two species (e.g. ≤ 20m or ≤ 50m in the wild [Terborgh, 1983; Whitesides, 1989; Podolsky, 1990] and ≤ 50cm in captivity [Leonardi et al., 2010; Buchanan-Smith et al., 2013] – see also Chapter 1), without further quantifying relationships between individuals. SNA has since been applied in single-species studies of *Sapajus* and *Saimiri* (e.g. Crofoot, 2011; Dufour et al., 2011; Claidière, Messer, Hoppitt & Whiten, 2013; Coelho et al., 2015), but as yet quantitative SNA studies on mixed-species groups have only been conducted on birds in mixed-species flocks (Farine, Garroway & Sheldon, 2012; Aplin, Farine, Morand-Ferron & Sheldon, 2012; Farine & Milburn, 2013; Farine, Aplin, Sheldon & Hoppitt, 2015; Marthy & Farine, 2018), fish affected by non-native species invasions (Beyer, Gozlan & Copp, 2010), and mixed-species savannah herbivores in the Masai Mara (Meise, Franks & Bro-Jørgensen, 2019).

Here I report an investigation of social structure, using SNA, for two mixed-groups of *Sapajus* and *Saimiri* at Living Links. The neighbouring enclosures, containing separate populations of *Sapajus* and *Saimiri* (West and East groups), create an opportunity to examine inter- and intra-group dynamics not only between the two species but also between the two sides. The groups have been studied together at Living Links since the facility opened in 2008 and have generally been observed to display low rates of both interspecific and intraspecific aggression (Leonardi et al., 2010; Dufour et al., 2011; Buchanan-Smith et al., 2013). Similarly, affiliative behaviours such as play, and grooming have been rarely observed between *Sapajus* and *Saimiri*, which follows observations made in the wild (e.g. Klein & Klein, 1973; Terborgh, 1983; Podolsky, 1990 - see also Chapter 2). Therefore, in terms of comparing single- and mixed-species networks it would be more meaningful to use spatial proximity (in line with previous studies in primate SNAs) as a proxy for network interactions/associations (e.g. Sade, 1989; Berman et al., 1997; Sueur & Petit, 2008; Ramos-Fernandez et al., 2009; Kasper & Voelkl, 2009; Lehmann & Ross, 2011; Zhang et al., 2012). Data collected from focal samples will allow for the inspection of factors that contribute to network position within (e.g. kinship, age, sex), and between species (e.g. age, rank). I asked to what extent network structure (i.e. stability) could be explained by dominance (within and between species) [Hypothesis, H1], kinship/relatedness [H2], and age-sex class [H3]. These hypotheses are not mutually exclusive, and I outline predictions for each in turn, based on previous literature.

In the wild, *Sapajus* and *Saimiri* have been reported as travelling and foraging in mixed-species groups (e.g. Fleagle & Mittermeier, 1981; Terborgh, 1983; Podolsky, 1990 – see also Chapter 1), and at Living Links both species have been found to spend an estimated 80% of their time in shared indoor and outdoor enclosures (see Buchanan-Smith et al., 2013 and Chapter 4). A review by Kasper and Voelkl (2009) presented findings from a network analysis of 70 primate groups (30 different species; 36 captivity; 28 wild), indicating that primate groups were generally high ($\bar{x}$=0.57, range=0.49–0.93). Therefore, it is expected that both species will be well connected in the network (e.g. high densities – see review in Kasper & Voelkl, 2009), producing one clear cluster in the sociogram (prediction 1.1). However, when considering the social and spatial separation observed between the two species in previous chapters (Chapters 4 & 5), it is predicted that the mixed-species networks will produce separate clusters for *Sapajus* and *Saimiri* (prediction 1.2). Concurrently, dominant/high ranking individuals tend to be more central in their networks compared to subordinates (e.g. Lusseau & Newman, 2004; Kanngiesser et al., 2011). *Sapajus* are approximately three times the size of *Saimiri* (see Chapter 1, Section 1.7 for general characteristics), and are noted as the dominant species in their associations in the wild (e.g. Fleagle & Mittermeier, 1981; Terborgh, 1983; Podolsky, 1990; Boinski, 1999), and as such it is predicted that *Sapajus* will generally have higher centrality measures compared to *Saimiri* in mixed-species networks (prediction 2). Additionally, lower ranking *Sapajus* may be more likely to be in proximity with *Saimiri* in order to reduce the chances of attack from more dominant individuals (e.g. shared vigilance, Hamilton, 1971; Alexander, 1974; van Schaik, 1983; Terborgh, 1983; Lee. 1994 – see also Chapter 5). Therefore, it is expected that there will be more ties between lower ranking *Sapajus* and *Saimiri* than with dominant individuals (prediction 3). Concurrently, due to *Sapajus* being dominant over *Saimiri* it is expected that there will be a greater difference in centrality measures for *Saimiri* compared to *Sapajus* between their single- and mixed-species networks, with the former producing higher centrality indices (prediction 4).

Kinship plays a key role in shaping animal societies, particularly in group-living species (e.g. Hinde, 1966, 1976; Kurland, 1975; Lee, 1994; Dunbar & Spoors, 1995; Silk, 2002; Hirsch, Stanton & Maldonado, 2012; Kurvers et al., 2013). For instance individuals are more likely to behave affiliatively (i.e. grooming, coalitionary support, tolerance, and food sharing) and consequently be in closer proximity to kin compared to non-kin (e.g. Kurland, 1975; Altmann, 1980; Koyama, 2003; Silk et al., 2004; Perry, Manson, Dower & Wikberg, 2003; Hirsch et al., 2012; Silk, Brosnan, Henrich, Lambeth & Shapiro, 2013; Smith, 2014). In species that exhibit female philopatry, dominance hierarchies are predominantly based on matrilineal rank inheritance (MRI), whereby offspring will generally inherit their position within the group’s social rank just below their mother (Kawamura, 1958; Lee & Oliver, 1979; Kutsukake, 2000; Hirsch, 2007; Hirsch et al., 2012). *Sapajus* live in multimale, multifemale groups organised by female philopatry and male dispersal (Fragaszy et al., 2004; Perry et al., 2004; Perry, Manson, Gros-Louis & Vigilant, 2008; Tiddi, Aureli, Schino & Voelkl, 2011; Rylands & Mittermeier, 2013 – see also Chapter 1). While *Saimiri* also live in multimale, multifemale groups, both sexes are organised by linear hierarchies and both will disperse from their natal groups (though females will typically remain during their first mating season – see Boinski, 1999; Boinski, Kauffman, Ehmke, Schet & Vreedzaam, 2005; Rylands & Mittermeier, 2013 – see also Chapter 1). Therefore, it is predicted that related individuals will be closely connected (i.e. high clustering coefficient) in their networks, with strong ties, and there will be a positive relationship between individuals who are related to high ranking individuals and centrality measures (prediction 5).

Furthermore, when considering age-sex class influences on the position of individuals within their social network, male *Sapajus* are typically dominant over females (with the exception of the alpha female - Fragaszy et al., 2004; Rylands & Mittermeier, 2013), therefore it is expected that males will score higher on centrality measures compared to females (prediction 6). Sex differences were not examined in *Saimiri* groups, because both contained only one male. Lastly, juveniles are also more likely to be engaged in high-energy activities such as play, compared to adults and are therefore more likely to be frequently in closer proximity (Lee & Oliver, 1979; Traylor-Holzer & Fritz, 1985; Wells & Turnquist, 2001; Heise & Moore, 2003; Hirsch, 2007; Limmer & Becker, 2007). Play behaviours have also been observed between juveniles of different species (e.g. Rudran, 1977; Struhsaker, 1981; Cords, 1987; Nakamura, 1997), including between juvenile *Sapajus* and *Saimiri* in captivity (Sodaro, 1999). Thus, it is expected that age will have a negative relationship with centrality measures in single- and mixed-species networks, and that juveniles will be important connectors (e.g. more ties) between the two species (prediction 7).

6.3 Methods

6.3.1 Subjects

This study was conducted at the Living Links (see Chapter 3). As mentioned in previous chapters, this research facility houses two separate mixed-species groups of squirrel monkeys (*Saimiri sciureus;* 26 individuals) and brown tufted capuchins (*Sapajus apella*; 35 individuals). Further details on individuals' genus, sex, age and group are provided in Tables 9.1-9.4 of Appendix I. Kinship (coefficients of relatedness =*r*) were estimated for each monkey based on known pedigree where parent-offspring relations *r*=0.5, full siblings *r*=0.5, half siblings r=0.25, for three quarter siblings (e.g. cases of inbreeding) *r*=0.375, grandparent-grandchild relations *r*=0.25, aunt/uncle/nephew/niece relations *r*=0.25, and first cousins and half aunt/uncle relations *r*=0.125. Kinship calculations are provided in Tables 9.5-9.8 of the Appendix VI.

6.3.2 Proximity measures

Providing a standard definition for what constitutes an association or being in social proximity is somewhat problematic due to the variation in environment/habitat, duration of associations and stability between different taxa (Heymann & Buchanan-Smith, 2000; Stensland et al., 2003). As discussed above, two or more species are considered to be in association when individuals of the different species are within a certain distance, such as ≤20m, ≤50m or ≤100 yds in the wild (Terborgh, 1983; Whitesides, 1989; Podolsky, 1990) and ≤50cm in captivity (Leonardi et al., 2010; Buchanan-Smith et al., 2013). For the purpose of this study, proximity between monkeys was measured in body lengths, with the baseline body length being ~40cm, based on the size of the largest monkey in the group. This measure was applied to both species in order to standardise the measure for the purpose of mixed-species measures. Proximity (nearest neighbours) was chosen as the network measure due to its use in previous research in studies on ungulates (Kimura, 1998; Wittemyer et al., 2005; Sundaresan et al., 2007; Stanley & Dunbar, 2013), cetaceans (Williams & Lusseau, 2006; Lusseau, 2007) and primates (e.g. Sade, 1972, 1989; Chepko-Sade & Sade, 1979; Sueur & Petit, 2008; Ramos-Fernández et al., 2009; Dufour et al., 2011; Lehmann & Ross, 2011; Crofoot et al., 2011; Zhang et al., 2012).

6.3.4 Behavioural sampling

One hundred and eighty-three hours of focal observations were recorded between April and August 2015, totalling three hours per individual spread across the five months. The monkeys were sampled evenly between 09:00 and 17:30, using instantaneous point sampling methods (Martin & Bateson, 2007). The focal was selected at random, and the observer (SD) would count 5 seconds before beginning recording to ensure that there was no bias in observed grouping(s) or behaviours. Each focal was recorded at 1-minute intervals for ten minutes and sampled 18 times over the study period. In each point sample, all group members (*Sapajus* and/or *Saimiri*) within two body lengths from the focal monkey were noted. If no monkey was within two body lengths, then the focal was described as being solitary. Two body lengths was used as a cut-off point for social proximity as it appeared that this was often the minimum distance that an individual allowed another individual to approach before they reacted (e.g. stay or move away; pers. obs.). Behaviours (major activities) of the focal and neighbours were also recorded at each interval (see Chapter 3,

Table 3.3 for behaviours and definitions). If a focal was out of sight for more than three minutes, then the focal was cancelled and re-sampled at another time.

6.3.5 Data analysis

Data for the social networks of the East and West groups were analysed using the compiled version of SOCPROG 2.9 (Whitehead, 2009). Although alternative network packages exist (e.g. *asnipe* in R – see Farine, 2013), SOCPROG was selected as it is widely used amongst ethologists making direct comparisons possible and is also currently the most user-friendly (Whitehead, 2008, 2009). Data were entered as group mode, which is where each row represents all individuals in proximity with the focal per point sample (10 points = 10 rows), along with supplementary information such as date and time (see Whitehead, 2009, p.10). Associations were defined in SOCPROG using a simple ratio index, as recommended by Whitehead (2009). A simple ratio index computes a figure between zero and one based on the number of times two individuals are seen together versus apart, and thus provides a direct measure of how closely associated each node is (Whitehead, 2009). Simple ratios are appropriate when all individuals can be equally sampled as together or not together at any point in time (Ginsberg & Young, 1982). Weighted proximity network diagrams were visualised in NetDraw in UCINET 6.0 (Borgatti, Everett & Freeman, 2002), using a principal coordinates arrangement of the data (see Whitehead, 2009). This produces an arrangement of points each representing an individual node, and the distance between them is proportional to one subtracted by the square root of their interaction rate (i.e. if the measure is asymmetric, the A-B interaction is the mean of the A-to-B and B-to-A interactions). Thus, individuals that interact frequently will be plotted together, while those that interact less frequently are plotted apart.

A node refers to an individual monkey and is displayed as a square or triangle in the network diagrams. An edge (i.e. a line) represents a proximity interaction between two or more nodes. Weighted networks were constructed, which indicates the frequency that a node was in proximity with another node (the weight of a tie is also known as its strength). Group density indicates the cohesiveness of a group and was calculated using the following formula (Scott, 2013 p.70):

$$\frac{l}{n(n-1)/2}$$

Where l represents the number of observed ties divided by the number of possible ties in the network (a density of 0 indicates no connections between individuals). The clustering coefficient measures the extent to which neighbours of a focal individual (or group) are clustered in space. Individuals with high clustering coefficient (CC) scores are linked with network stability, for instance if an individual with high CC is removed from the group then there is a higher probability that the observed associations will no longer show the same linkage, thus disrupting network stability (Hanneman & Riddle, 2005). The group mean value of CC was calculated as an estimate of the level of network stability. Degree centrality (how many direct ties an individual node has with other nodes – see Table 6.1), indicates the prominence or importance of a node within a network, as such, individuals with higher scores are likely to be more central (Whitehead, 2009). Betweenness centrality refers to the number of shortest paths that pass through a focal individual, with the shortest path being the shortest distance. If there is little difference in betweenness scores across nodes, then the removal of individuals will have little impact on the network structure. In contrast to this, if there is a large variation in betweenness scores across nodes, then the removal of an individual can substantially impact the network structure (e.g. Flack, Girvan, de Waal & Krakauer, 2006; Coleing, 2009). Eigenvector centrality represents the number and strength of connections of an individual, as well as the number and strength of the individuals that they are connected to. Individuals with high eigenvector centrality will have relatively strong associations to other individuals, which in turn have relatively strong associations with others (Croft et al., 2008; Whitehead, 2009).

The following statistical tests were performed using the software package R (version 3.6.3) in the RStudio environment (R Core Team, 2020; RStudio, 2020 – see code here https://osf.io/6fph5/). Spearman correlations were used to examine the relationship between network properties (including strength, eigenvector centrality and clustering coefficient) and age, kinship and node degree. Wilcoxon signed rank tests were used to examine the variation in centrality and clustering coefficient scores between *Sapajus* and *Saimiri* and between single and mixed-species networks. Figures were produced using Microsoft Excel 2019.

6.4 Results

The overall network connectivity for the West and East groups were low for both single- and mixed-species networks. For West *Sapajus*, group density was 0.16, containing only 4502 connections out of a possible 27540 among all 18 nodes. In contrast the West *Saimiri* had slightly higher group density 0.34, based on 2232 connections out of a possible 6480; however this could be attributed to there being an increased probability of being associated with others (as a function of *N* possible associates) in a smaller group (*N*=9 nodes). East *Sapajus* and *Saimiri* group densities were equally low, 0.15 (3614 connections) and 0.12 (3041 connections) respectively out of a possible 24480 connections based on 17 nodes. Results for mixed-species network connectivity were smaller still, with the West group resulting in a group density of 0.11, containing 6805 connections out of a possible 63180, based on 27 nodes and the East group density of 0.07, 7016 connections out of a possible 100980 based on 34 nodes. Sociograms for single-species networks for the West and East groups are provided in Figures 6.1 and 6.2 respectively, and mixed-species networks in Figure 6.3.

Clustering coefficients (*CC*) varied (range: 0.11–0.46) for the West *Sapajus* single-species network ($\bar{x}$=0.244, ±SE=0.108), with the following individuals identified as having high scores (*CC*=0.46, ±SE=0.03 – see Table 9.11 in Appendix VII): the alpha male Diego, alpha female Lana and Santiago (eldest daughter of alpha female), indicating that if any or all of these individuals were to be removed from the group then this could negatively impact on network stability. The individuals named above also scored highly for eigenvector centrality (*EC*) compared to the rest of the group ≤0.1 (see Table 9.11 in Appendix VII): Diego (*EC*=0.33, ±SE=0.31); Lana (*EC*=0.41, ±SE=0.19); and Santiago (*EC*=0.38, ±SE=0.17). The four juveniles (<2yrs) of the group also received high *EC* scores: Mr Fudge (*EC*=0.42, ±SE=0.19); Bear (*EC*=0.39, ±SE=0.18); Pixie (*EC*=0.38, ±SE=0.18) and Hazel (*EC*=0.23, ±SE=0.10). The positions and the thickness (strength) of ties between the above individuals in the sociogram (Figure 6.1A), indicate that they were frequently observed in proximity.

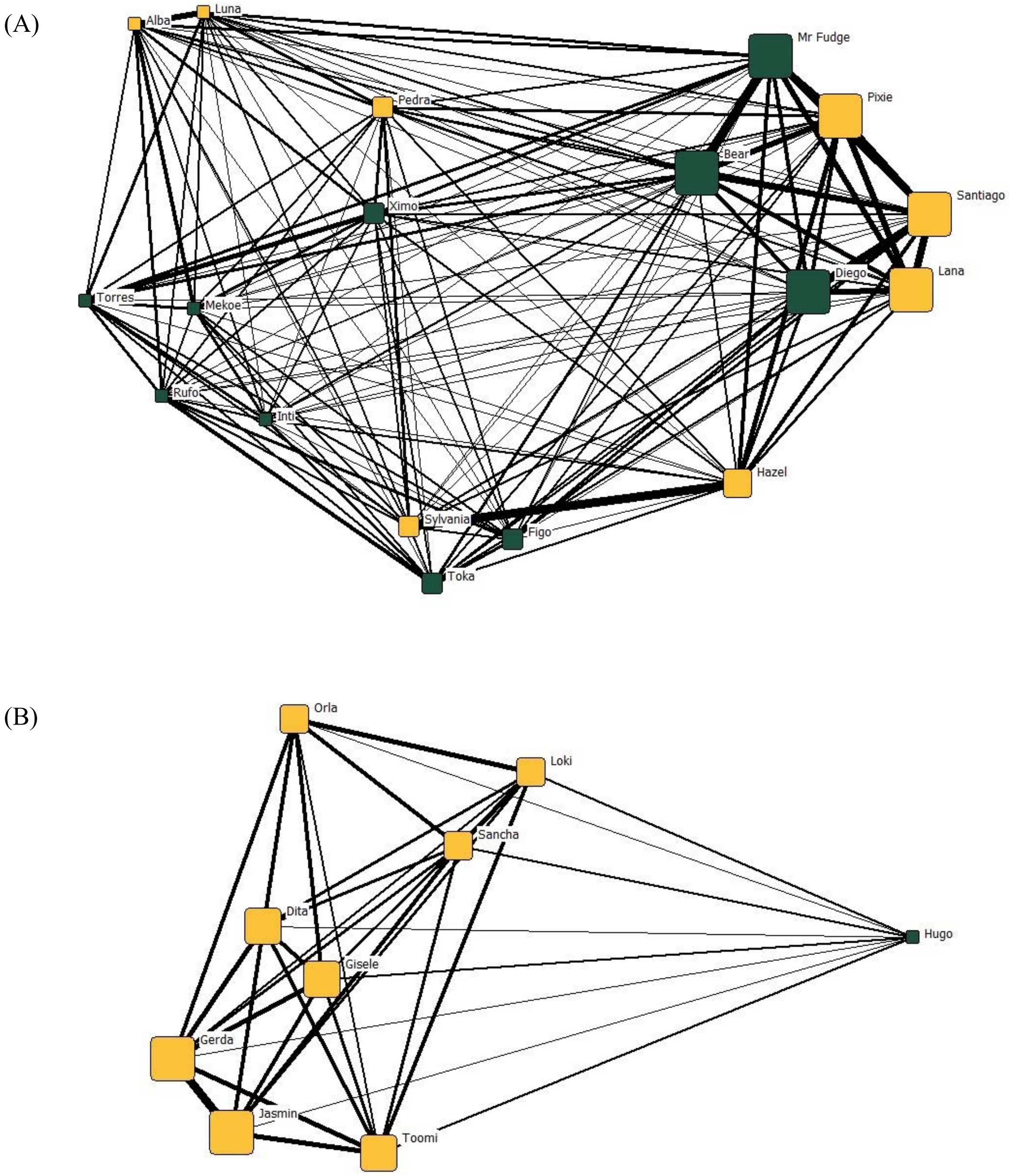
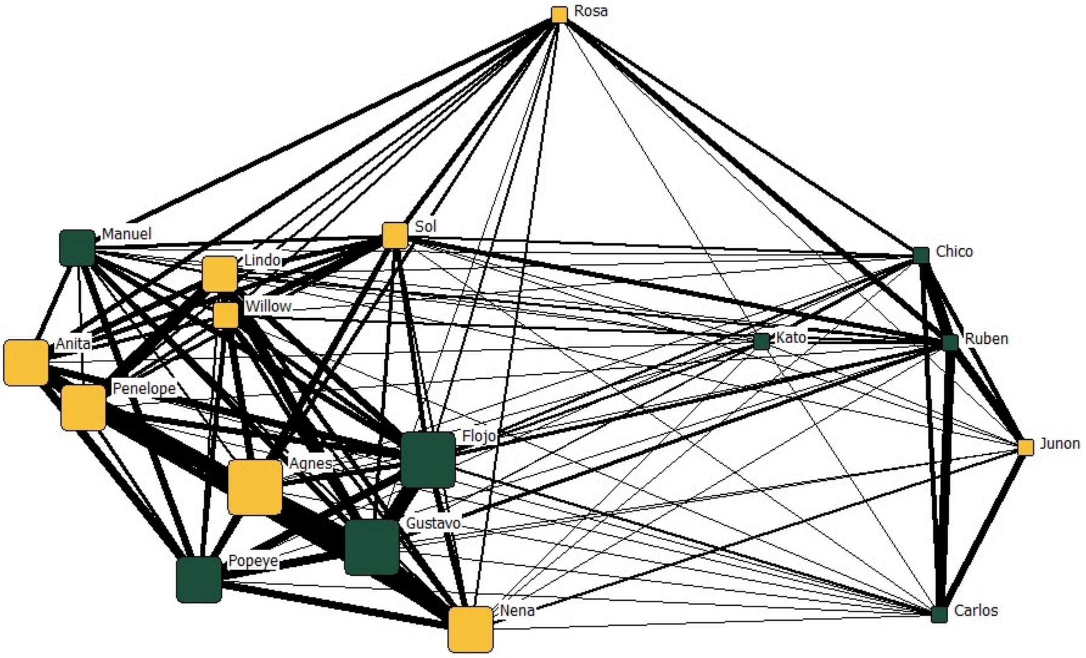


Figure 6.1 Illustration of the social networks for the West (A) *Sapajus* and (B) *Saimiri*. This produces an arrangement of points each representing an individual node, and the distance between them is proportional to one subtracted by the square root of their interaction rate (i.e. if the measure is asymmetric, the A-B interaction is the mean of the A-to-B and B-to-A interactions). Node size is proportional to eigenvector centrality, node colour indicates sex (yellow = female; green = male), and strength of ties is based on frequency of interactions between nodes. The alpha male for West *Sapajus* is Diego and alpha female is Lana. The alpha/only male in the West *Saimiri* is Hugo.

(A)



(B)

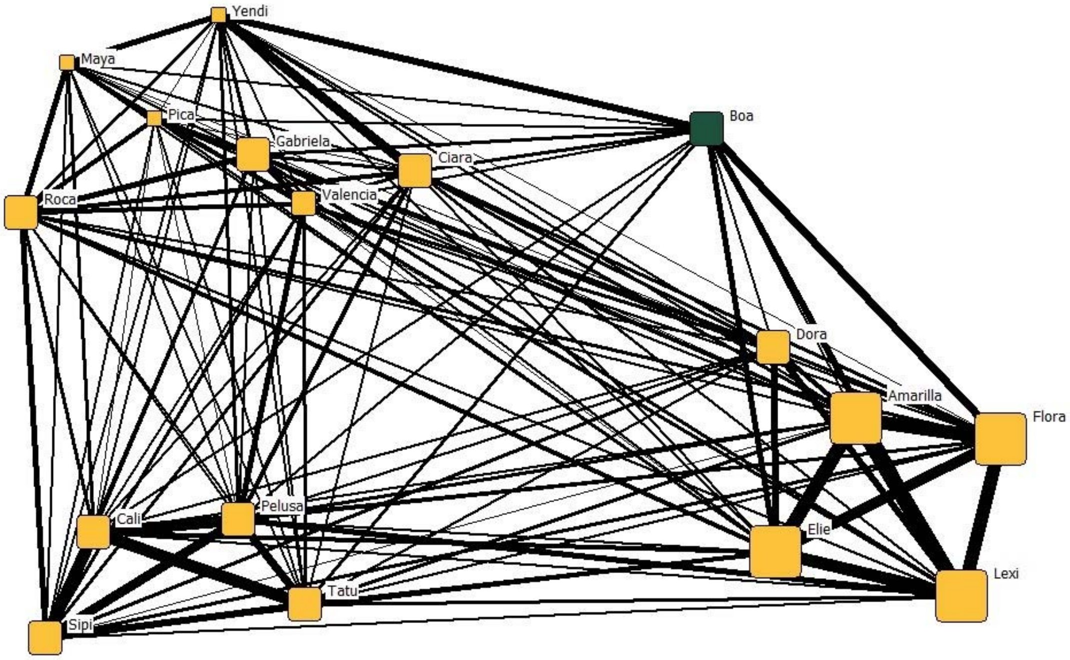


Figure 6.2 Illustration of the social networks for the East (A) *Sapajus* and (B) *Saimiri*. This produces an arrangement of points each representing an individual node, and the distance between them is proportional to one subtracted by the square root of their interaction rate (i.e. if the measure is asymmetric, the A-B interaction is the mean of the A-to-B and B-to-A interactions). Node size is proportional to eigenvector centrality, node colour indicates sex (yellow = female; green = male), and strength of ties is based on frequency of interactions between nodes. The alpha male for East *Sapajus* is Popeye and alpha female is Anita. The alpha/only male in the East *Saimiri* is Boa.

Individuals with lower *EC* appear to be forming smaller subgroups within the network (4 subgroups identified), for instance there is a bachelor group formed of the following individuals Mekoe, Inti, Rufo and Torres, which have been placed at a distance (opposite side of the network) from the alpha male and female (see Figure 6.1A). This difference in placement, indicates low interactions with the cluster containing the alpha male and female, and could be an indicator of which individuals are subordinate/low ranking. In contrast there was less variation (range: 0.31–0.39) in *CC* ($\bar{x}$=0.364, ±SE=0.009) and *EC* ($\bar{x}$=0.31, ±SE=0.04) for the West *Saimiri* single-species network, indicating that network would not be greatly affected if an individual were removed. The individual with the highest *EC* was Gerda (*EC* =0.44, ±SE=0.22), which could indicate that she is the dominant female of the group (she is also the oldest at 15 years of age). The lowest *EC* was found for the alpha male Hugo (*EC* =0.05, ±SE=0.46); despite his degree centrality (8) and the sociogram (Figure 6.1B) showing that he is connected with all other individuals, the strength of ties was quite weak and he was quite clearly peripheral to the rest of the group. However, this may be attributed to Hugo spending a high proportion of time during observations on his own in areas where he could not be seen from any of the viewing platforms.

CC varied (range: 0.12–0.44) for the East *Sapajus* single-species network ($\bar{x}$=0.326, ±SE=0.023), with similar individuals as the West *Sapajus* group identified as having high scores: the alpha male Popeye (*CC*=0.40, ±SE=0.03), alpha female Anita (*CC*=0.37, ±SE=0.03), and the eldest daughter of the alpha female Penelope (*CC*=0.40, ±SE=0.03). The beta male Manuel was found to have the highest score (*CC*=0.41, ±SE=0.03), which is interesting as this does not correspond with his *EC*, which was relatively low (*EC*=0.21, ±SE=0.10) compared to the previously mentioned individuals. Regardless, the results of the *CC* suggest that if any or all of these individuals were to be removed from the group then it could potentially have a negative impact on network stability, as group dynamics and relationships would likely change. As with the West *Sapajus*, the alphas and eldest daughter to the alpha female for the East group also scored highly for *EC* (Popeye: *EC*=0.30, ±SE=0.33; Anita: *EC*=0.30, ±SE=0.14; and Penelope: *EC*=0.33, ±SE=0.16), as well as the juveniles (≤2yrs) of the group (Nena: *EC*=0.32, ±SE=0.15; Gustavo: *EC*=0.42, ±SE=0.2; and Agnes: *EC*=0.35, ±SE=0.16) and one subadult (3.5yrs) male (Flojo: *EC*=0.37, ±SE=0.17). All individuals with high *EC* were frequently observed in proximity, which can be seen in the sociogram (Figure 6.2A) based on the position and thickness (strength) of ties. The network indices and sociogram also indicate that there may be a small subgroup within

East *Sapajus* consisting of an unrelated adult female Junon and her matrilineal line (Carlos, Chico and Ruben), along with Kato (wild caught and unrelated male) who has stronger connections with the males from this subgroup compared to the main cluster. Within the group network Junon has low *EC* (0.02, ±SE=0.01); however she has a high *CC* (0.31, ±SE=0.05) which could indicate her importance for the stability of the subgroup network. A young adult female Rosa appears as a lone peripheral individual in the sociogram (Figure 6.2A); this may be due to her having relatively strong ties with both subgroups, which may be indicative of her as an important individual in the network for the maintenance of group network stability. However, her comparatively low *CC* (0.22, ±SE=0.02) to the rest of the group ($\bar{x}$=0.33) would suggest that this is not the case.

CC scores for the East *Saimiri* ($\bar{x}$=0.25, ±SE=0.023) also varied (range: 0.13–0.40). Similar to the West *Saimiri* single-species network, the alpha male for the East *Saimiri*, Boa (*EC*=0.15, ±SE=0.40) was peripheral and had relatively low *CC* (0.24, ±SE=0.02) as well as low *EC* (*EC*=0.15, ±SE=0.40), though not the lowest (see Table 9.14 in Appendix VII). Individuals with high *CC* and *EC* appear to come from Elie's (*CC*=0.37, ±SE=0.02; *EC*=0.40, ±SE=0.19) matrilineal line: Flora (*CC*=0.40, ±SE=0.02; *EC*=0.4, ±SE=0.19); Lexi (*CC*=0.38, ±SE=0.03; *EC*=0.43, ±SE=0.20); and Amarilla (*CC*=0.39, ±SE=0.03; *EC*=0.43, ±SE=0.20). This may indicate that Elie is the dominant female for the East *Saimiri* and that her removal from the network may disrupt the group network, as group dynamics and relationships would likely change.

There are distinct differences between the mixed-species sociograms for the West and East groups (Figure 6.3). For the West groups, the species are clearly separated into two clusters, and although there are some ties between them, they appear to have low strength, indicating that the two species were rarely observed in proximity. There was a significant difference in *EC* (Mann Whitney U, W=162, p <0.0001, r=0.813) and *CC* (W=41.5, p=0.044, r=0.387) between the West monkeys in the mixed-species network, with higher mean scores for *Sapajus* (*EC*: $\bar{x}$=0.182, ±SE=0.029; *CC*: $\bar{x}$=0.229, ±SE=0.026) compared with *Saimiri* (*EC*: $\bar{x}$=0.0, ±SE=0.0; *CC*: $\bar{x}$=0.354, ±SE=0.032).

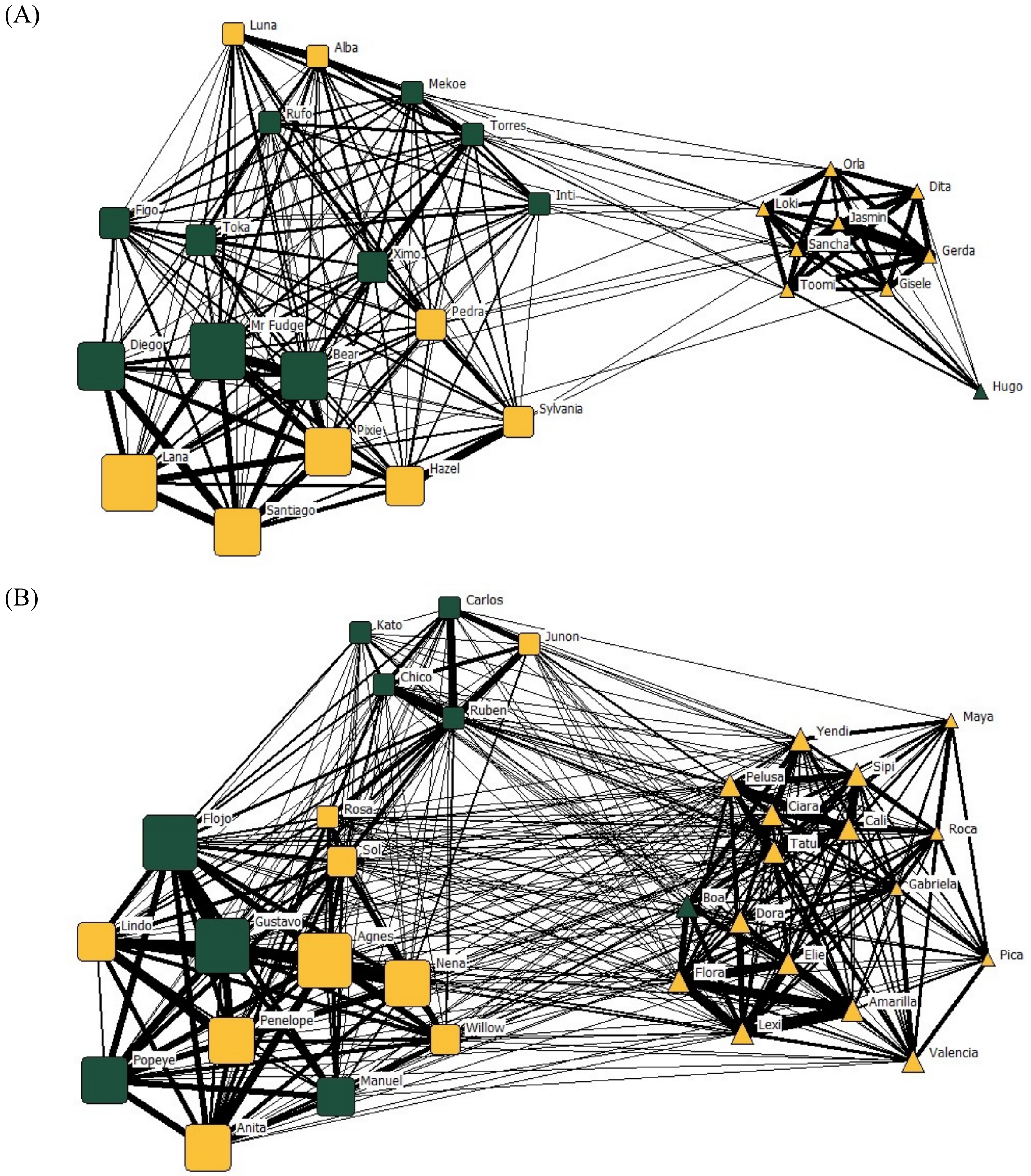


Figure 6.3 Illustration of mixed-species social networks for the (A) West and (B) East groups. This produces an arrangement of points each representing an individual node, and the distance between them is proportional to one subtracted by the square root of their interaction rate (i.e. if the measure is asymmetric, the A-B interaction is the mean of the A-to-B and B-to-A interactions). Node size is proportional to eigenvector centrality, node colour indicates sex (yellow = female; green = male) and node shape is based on species: *Sapajus* = square and *Saimiri* = triangle. Strength of ties is based on frequency of interactions between nodes.

The proximal separation between the two species is also demonstrated in the East mixed-species network, with a significant difference in *EC* (Mann Whitney U, $W = 261$, $p < 0.0001$, $r = 0.693$) and *CC* ($W = 216$, $p = 0.014$, $r = 0.420$) between the East monkeys mixed-species network, with higher mean scores for *Sapajus* (*EC*: $\bar{x} = 0.200$, ±SE=0.034; *CC*: $\bar{x} = 0.289$, ±SE=0.025) compared with *Saimiri* (*EC*: $\bar{x} = 0.023$, ±SE=0.003; *CC*: $\bar{x} = 0.209$, ±SE=0.019). However, there are more ties between species, demonstrating higher strength in the East mixed-species network compared to the West (see Figure 6.3). These differences in inter-species connections may be due to the difference in the frequency of occurrences in which the West *Saimiri* were observed in shared enclosures. Despite the network analyses accounting for *N* of the observations made (West: $n = 1627$ point samples; East: $n = 3147$ point samples), the West *Saimiri* were rarely observed in either the outdoor enclosure (18%) or *Sapajus* indoor enclosure (1%), compared to the East *Saimiri*, who were observed in shared enclosures for just over half of focal follows (outdoors=34%; *Sapajus* indoor=20%). Furthermore, the higher scores in *EC* and *CC* between species suggest that *Sapajus* are more central and dominant over *Saimiri* in mixed-species networks.

The mean (±SE) network degree, (i.e. the mean number of individuals directly connected by proximity interactions (ties) to each individual/node), betweenness centrality and eigenvector centrality were calculated for each single-species and mixed-species network and are presented in Table 6.2. Both centrality indices correlated significantly with node degree for East *Sapajus* (betweenness: $r_s = 0.804$, $N = 17$, $p < 0.0001$; eigenvector centrality: $r_s = 0.500$, $N = 17$, $p = 0.041$) and West mixed-species (betweenness: $r_s = 0.421$, $N = 27$, $p = 0.029$; eigenvector centrality: $r_s = 0.487$, $N = 27$, $p < 0.01$), which may suggest that nodes with higher centrality were likely to be in proximity with a greater number of nodes. However, this finding was not consistent with all datasets, as no significant relationships were found for West *Saimiri*. There was also no significant relationship found between eigenvector centrality and node degree for West *Sapajus,* East *Saimiri* or East mixed-species. However, there was a significant relationship found for betweenness and node degree: (West *Sapajus*: $r_s = 0.976$, $N = 18$, $p < 0.0001$; East *Saimiri*: $r_s = 0.996$, $N = 17$, $p < 0.0001$; East mixed-species: $r_s = 0.942$, $N = 34$, $p < 0.0001$).

Table 6.2 *Mean (±SE) node degree and centrality indices for West and East single-species and mixed-species networks.*

	Node degree	**Betweenness centrality**	**Eigenvector centrality**
West *Sapajus*	16.556 (±0.145)	0.222 (±0.012)	0.182 (±0.036)
West *Saimiri*	8.000 (±0.000)	~0.000 (±0.000)	0.313 (±0.038)
West mixed	15.333 (±0.753)	6.111 (±1.225)	0.121 (±0.029)
East *Sapajus*	14.235 (±0.369)	0.882 (±0.094)	0.202 (±0.141)
East *Saimiri*	15.765 (±0.136)	0.118 (±0.014)	0.209 (±0.030)
East mixed	0.249 (±0.692)	4.412 (±0.414)	0.111 (±0.023)

Overall, sex was not found to be a significant contributor to *EC* or *CC* for either of the *Sapajus* groups (*p*>0.05) and was not examined in *Saimiri* due to there being only one adult male in each group. Age and kinship were found to be positively correlated with eigenvector centrality in the West *Saimiri* (see Table 6.3). While this may indicate that older individuals who are related are more central, this effect was not found across the groups, which may be due to there being a smaller *Saimiri* group (*N*=9) in the West with two matrilines who happen to be siblings (Gerda and Jasmin) and a younger weakly connected alpha male. However for East *Sapajus* kinship was also found to have a significantly positive relationship with eigenvector centrality as well as clustering coefficient (see Table 6.3), which may be due to there being the two matrilines (Anita and Junon), that can be viewed as separate clusters in the sociogram (Figure 6.2A).

Table 6.3 *Spearman correlation coefficients of age and kinship with eigenvector centrality and clustering coefficient for West and East single-species and mixed-species groups. Kinship was not analysed for mixed-species networks as* Sapajus *and* Saimiri *are unrelated.*

		WEST			**EAST**		
		Sapajus	***Saimiri***	**Mixed**	***Sapajus***	***Saimiri***	**Mixed**
Eigenvector centrality	**Age**	0.001ns	0.756*	0.017ns	-0.466ns	-0.146ns	-0.282ns
	Kinship	0.022ns	0.871**	---	0.693***	0.272ns	---
Clustering coefficient	**Age**	0.185ns	0.363ns	0.16ns	-0.120ns	-0.159ns	-0.108ns
	Kinship	-0.018ns	0.665*	---	0.539*	0.310ns	---

**p*<0.05, ***p*<0.01, ****p*<0.001, ns>0.05

No significant difference in *EC* was found between West *Sapajus* (Wilcoxon signed rank: Z=NaN, p=NA) single-species and mixed-species networks (*EC*: $\bar{x}=0.182$, ±SE=0.078); however there was a difference found for *CC* ($Z=-3.626$, $p<0.0001$, $r=0.855$), with higher values in the single-species network (*CC*: $\bar{x}=0.244$, ±SE=0.108) compared with the mixed-species network (*CC*: $\bar{x}=0.229$, ±SE=0.026). As predicted, the West *Saimiri* scored significantly higher in *EC* ($Z=-2.609$, $p<0.01$, $r= 0.87$) and *CC* ($Z=-2.439$, $p=0.015$, $r=0.813$) in their single-species network (*EC*: $\bar{x}=0.313$, ±SE=0.038; *CC*: $\bar{x}=0.364$, ±SE=0.009) compared to the mixed-species network (*EC*: $\bar{x}=0.00$, ±SE=0.00; *CC*: $\bar{x}=0.354$, ±SE=0.032). Similarly, to the West *Sapajus EC* scores did not vary significantly ($Z=-1.443$, $p=0.149$, $r=0.35$) for East *Sapajus*, indeed the mean score for *EC* ($\bar{x}=0.202$, ±SE=0.034) was the same for both single-species and mixed-species networks. However, a difference was found between single-species ($\bar{x}=0.325$, ±SE=0.023) and mixed-species ($\bar{x}=0.289$, ±SE=0.025) networks for *CC* ($Z=-3.605$, $p<0.001$, $r=0.873$). East *Saimiri* were also found to have higher *EC* ($Z=-3.599$, $p<0.001$, $r=0.87$) and *CC* ($Z=-3604$, $p<0.001$, $r=0.874$) values when in single-species networks (*EC*: $\bar{x}=0.209$, ±SE=0.031; *CC*: $\bar{x}=0.250$, ±SE=0.023) compared to mixed (*EC*: $\bar{x}=0.023$, ±SE=0.003; *CC*: $\bar{x}=0.209$, ±SE=0.081). Overall *EC* scores only seemed to change substantially for *Saimiri* and although there were differences in *CC* between networks, all individuals who had high *CC* in their single species network were still high in the mixed-species network.

6.4 Discussion

Social network analyses (SNAs) indicated that individual network positions and centrality indices were strongly determined by species identity (*Sapajus/Saimiri*). As predicted (prediction 1.2), the mixed-species networks produced separate clusters for *Sapajus* and *Saimiri* (Figure 6.3) in both the West and East groups. The division between the species in the mixed social networks is consistent with findings in previous chapters, where the monkeys' were utilising different areas of shared enclosures (*Saimiri* on the periphery and *Sapajus* in more central zones – see Chapter 4), and were found to be asynchronous in their behaviours (Chapters 5). SNAs demonstrated that there were few ties between species in the West group, which is likely because the two species were rarely in proximity, as *Saimiri* were hardly ever observed in shared enclosures (outdoor: 18%, *Sapajus* indoor: 1%). In contrast, the East groups had more ties between species, the strength of ties was greater than in the West mixed-species network (see Figure 6.3), and they were observed for over half of focal observations in shared enclosures (outdoors=34%; *Sapajus* indoor=20%). Yet, despite the East groups spending time in shared enclosures, and therefore the right circumstances to be in proximity, they were still shown to be two separate groups in the mixed-species sociogram (Figure 6.3) as well as centrality indices (see Tables 9.9-9.14 in Appendix VII). This network separation between species may be attributed to overall network connectivity, which was found to be sparse for both West and East single- and mixed-species networks, with low group densities (West: *Sapajus*=0.16; *Saimiri*=0.34; mixed=0.11; East: *Sapajus*=0.15; *Saimiri*=0.12; mixed=0.07). While low densities may have been expected for mixed-species networks (prediction 1.2), the density found for single-species networks is substantially lower than findings in other primate species ($\bar{x}$=0.57, range=0.49–0.93 for 70 primate groups across 30 species – see review in Kasper & Voelkl, 2009). Thus, in addition to my previous findings, SNA has shown that the monkeys are living as two separate groups that occasionally and only temporarily are in close enough proximity to have the potential to interact physically (at least for the East group).

Eigenvector centrality (EC) highlighted which individuals were central or peripheral, in addition to individuals who may be important for maintaining group network stability. Both the West and East *Sapajus* alpha male and alpha female had high EC which is consistent with previous findings in *Sapajus* networks (Dufour et al., 2011; Tiddi et al., 2011; Morton, 2014). Comparatively the alpha male in both *Saimiri* groups had quite low EC, which is also consistent with previous findings in *Saimiri* social networks (Dufour et al., 2011; Claidière et al., 2013). With regard to mixed-species social networks, as expected (Prediction 2) *Sapajus* were found to have higher EC than *Saimiri* in the mixed-species networks (see Figure 6.3 and Tables 9.9 and 9.10 in Appendix VII). Consequently, there were significantly greater differences in centrality measures between *Saimiri* single-species networks than for *Sapajus*. These differences were particularly marked for the West groups, where *Sapajus* EC did not vary between single- and mixed-species networks (see Tables 9.9 and 9.11 in Appendix VII). While *Saimiri* were found to be barely connected in the mixed-species network (EC~0.00, see also Figure 6.3A), supporting my prediction that there would be a greater difference in *Saimiri* centrality scores between single- and mixed-species networks (prediction 4). However, as mentioned previously this was due to *Saimiri* rarely choosing to spend time in shared enclosures and therefore rarely coming into proximity with *Sapajus*. The pattern was similar for the East groups, with EC not varying between networks for

Sapajus, and *Saimiri* were found to be less well connected in the mixed-species network compared to their single-species network (see Tables 9.10, 9.13 and 9.14 in Appendix VII), but unlike the West *Saimiri* their EC scores were similar to peripheral *Sapajus*, providing support for prediction three. For instance, Boa (alpha male *Saimiri*) and Kato (unrelated peripheral male *Sapajus*) both had an EC score of 0.02 compared to Popeye (alpha male *Sapajus*) whose EC was 0.30.

Therefore, in addition to EC being an indicator for how well an individual is associated to other well associated individuals, it may also suggest which individuals are dominant in the group. Indeed, previous primate studies have found that social rank is positively correlated with EC (e.g. Lusseau & Newman, 2004; Kanngiesser et al., 2011; Morton, 2014; Wang et al., 2015). Thus, when considering *Saimiri*, who do not have a clearly distinguishable alpha female as do *Sapajus* (e.g. Boinski, 1999; Boinski et al., 2005; Fragaszy et al., 2004; Rylands & Mittermeier, 2013 – see also Chapter 1), but form linear dominance hierarchies, *EC* can help to determine which individuals are dominant/high-ranking. In the East *Saimiri* group Elie and her offspring (see Appendix VI and Appendix VII) all have comparatively higher EC (range=0.4-0.43) than the rest of the group (EC: range=0.06-0.24) indicating dominance based on matrilineal rank inheritance (e.g. Kawamura, 1958; Lee & Oliver, 1979; Kutsukake, 2000; Hirsch, 2007; Hirsch et al., 2012). Similarly, in the West *Saimiri* group, Gerda and her offspring appear to have marginally higher EC compared to the other females in the group (see Appendix VI and Appendix VII).

For the most part *Sapajus* with high EC also scored highly for clustering coefficient (CC) in both single-species and mixed-species networks, for example the *Sapajus* alpha males and females for West (both networks - Diego - EC=0.33, CC=0.44; Lana: EC=0.41, CC=0.44) and East *Sapajus* (Popeye - single-species network: EC=0.30, CC=0.40; mixed-species network: EC=0.30, CC=0.38; Anita - single-species network: EC=0.30; CC=0.37; mixed-species network: EC=0.29; CC=0.35). Similarly, individuals who had low EC also received low scores in CC in both single- and mixed-species networks, such as the second eldest daughters of the alpha female's in both groups West (Sylvania - single-species network: EC=0.07; CC=0.13; mixed-species network: EC=0.07; CC=0.12) and East (Rosa - single-species network: EC=0.08; CC=0.22; mixed-species network: EC=0.08; CC=0.17). However, when looking at the single-species network for East *Sapajus*, there were two individuals in particular who, despite having relatively low EC, had high CC scores (high

CC is an indicator of an individual's importance to group network stability): the beta male Manuel (EC=0.21; CC=0.41) and Junon (EC=0.02; CC=0.31). While *Saimiri* EC were much lower in mixed-species networks compared to single-species, their CC did not change as dramatically (see Appendix VII), which is expected as *Saimiri* are still important in relation to network stability and cohesiveness in their own subgroup.

It may be expected that since Manuel is the son of the alpha female (Anita), matrilineal (inherited) social rank may factor into this higher CC, however the beta male(s) for the West group (unclear whether Toka or Figo) had low EC and CC, despite being the offspring of the alpha female (Lana). This difference may be attributed to Manuel behaving in a manner that suggested he was in the process of attempting to displace Popeye as the alpha male of the group. I witnessed similar behaviour in Popeye before he displaced Maurice as the alpha male when I was collecting data in 2009. Not only were Manuel's behaviours similar, but physically he looked larger. Perhaps Manuel was observed more frequently in proximity with other members of the group in order to form alliances or potential agonistic support, as observed in other studies on Cebus/*Sapajus* (Fragazy et al., 2004; Perry et al., 2004, 2008; Tiddi et al., 2011). Thus, SNA could be applied to long-term studies on group structure (and stability) in order to monitor changes in dominance hierarchies and group dynamics (Buchanan-Smith et al., 2013; Rose & Croft, 2015). In contrast Junon is an adult female who is not related to the alpha female (Anita), which may be why she has fewer ties (low strength) with the main cluster (see Figure 6.3), and concurrently has low EC. Despite this, she has strong ties with her sons (i.e. is frequently observed in proximity - see Figure 6.2A) and has a high CC score (see above), though not the highest for East *Sapajus*, her removal may still impact group network stability. However, upon examining whether relatedness would be positively correlated with centrality measures (prediction 5), support was only found for the East *Sapajus* and West *Saimiri* groups (see Table 6.3). This finding is compatible with previous research that individuals will generally be in closer proximity to kin compared to non-kin (e.g. Kurland, 1975; Altmann, 1980; Koyama 2003; Silk et al., 2004, 2013; Perry et al., 2003; Hirsch et al. 2012; Smith 2014), for instance in the East *Sapajus* group there are two matrilines (i.e. Anita and Junon) that are separated into two distinct clusters in the network diagram (see Figure 6.2A). The differences between groups could be attributed to the network being based solely on proximity irrespective of behaviours/interactions. Typically, individuals will behave more affiliatively with kin (i.e. grooming, coalitionary support, tolerance, and food sharing) than non-kin and consequently be in closer proximity, which likely explains the strong ties between kin within single-species and mixed-species networks. However if the network is not solely focussed on affiliative behaviours then individuals may also be coming into closer proximity with individuals (generally non-kin) via aggressive (e.g. contact aggression, chase, displacement) and/or neutral interactions (e.g. moving towards another individual(s) but shows no interest in interacting or simply passing to go elsewhere – see Leonardi et al., 2010; Buchanan-Smith et al., 2013). Therefore, more general networks based on proximities rather than specific interactions (i.e. affiliative, aggressive or neutral), can provide a more general overview of the frequency of interactions between individuals (e.g. Crofoot et al., 2011).

Contrary to prediction 6, sex was not found to have a significant influence on the position of *Sapajus* within their single-species networks ($p>0.05$). While this finding is incompatible with literature on *Sapajus* social organisations, which stipulate that males are dominant over females (e.g. Fragaszy et al., 2004; Rylands & Mittermeier, 2013 – see also Chapter 1), it does complement previous research on primate social networks where sex was not found to affect network centrality (e.g. Crofoot et al., 2011; Morton, 2014; Pasquaretta et al., 2014). Similarly, age was not found to have a significant influence on centrality measures, which complements the findings of previous studies (e.g. Dufour et al., 2011; Tiddi et al., 2011; Morton, 2014). However, contrary to prediction seven, a positive correlation was found for the West *Saimiri* group (see Table 6.3), which could be attributed to a greater extreme in age range (N=9; 1-15years) with a higher proportion of older individuals compared to the East group (N=17; age range=3-14). Furthermore, when examining whether juveniles were important connectors in mixed-species networks, the sociogram for the East group show juvenile *Sapajus* as well as peripheral individuals (Junon's cluster, Rosa and Sol) with mostly adult *Saimiri* rather than juveniles (see Figure 6.3B). In contrast, the sociogram for the West mixed-species (Figure 6.3A) indicate that the majority of ties were between peripheral *Sapajus* (i.e. low ranking due to low EC) and juvenile/sub-adult *Saimiri*. While these results contradict Sodaro's (1999) findings that captive juvenile *Sapajus* and *Saimiri* interacted more frequently than adults, they do provide further support for prediction three; that lower ranking *Sapajus* may be more likely to be in proximity with *Saimiri*. The lack of ties between juveniles could simply be due to the monkeys not being observed frequently in proximity during focal follows (but could have been at other times – see Brando & Buchanan-Smith, 2018) or due to a low rate of play compared with other behaviours that make up the majority of daily activity budgets (e.g. vigilant, foraging, resting etc).

Although there are previous studies investigating mixed-species social networks (e.g. mixed flocks: Farine et al., 2012, 2015; Alpin et al., 2012; Farine & Milburn, 2013; fish assemblage: Beyer et al., 2010; savannah ungulates: Meise et al., 2019), to my knowledge this is the first study that has examined mixed-species social networks in captive groups of *Sapajus* and *Saimiri*. The 'groupness' of *Sapajus*-*Saimiri* mixed-species groups (both wild and captive) has typically been determined by the frequency and duration of interactions at the group-level (e.g. Klein & Klein, 1973, 1975; Fleagle & Mittermeier, 1981; Mittermeier & van Roosmalen, 1981; Terborgh, 1983; Podolsky, 1990; Leonardi et al., 2010; Buchanan-Smith et al., 2013; Levi et al., 2013 – see also Chapter 1). What is special about the application of SNAs to mixed-species research is that relative to other group members, each individual's connections (with all other group members) can be robustly statistically described simultaneously. The results of this study raise some exciting and interesting questions about what we currently know about the dynamics and social structure of *Sapajus*-*Saimiri* mixed-species groups, at least within the captive environment. When considering the differences in the monkey's use of space in shared enclosures (Chapter 4), and the asynchronicity of their behaviours (Chapter 5), in conjunction with the SNA findings, the results resoundingly point towards them being two separate groups, that happen to live together in a mixed-species exhibit, and occasionally interact with each other.

Field research often describe *Sapajus* and *Saimiri* as mixed-species groups (e.g. Klein & Klein, 1973; Fleagle & Mittermeier, 1981; Mittermeier & van Roosmalen, 1981; Terborgh, 1983; Podolsky, 1990; Levi et al., 2013 – see also Chapters 1 & 2), and perhaps this still holds true as there could be a number of additional environmental factors (e.g. habitat, seasonality, risk of predation, competition for resources etc) that could be contributing to groupness, which cannot be completely replicated in captivity. The captive setting of the study groups limit the capacity to generalise the obtained results to wild groups; however, *Sapajus* and *Saimiri* are very difficult to follow in the wild and captive studies provide better opportunities to investigate their social behaviour. One way to potentially overcome this, is to carefully consider enclosure design, especially in a mixed-exhibit, whereby species-appropriate substrates are provided (see Leonardi et al., 2010; Buchanan-Smith et al., 2013 – see also Chapter 4). For instance, large bushes to replicate the understory for *Saimiri* and tall trees with adequate horizontals for *Sapajus*.

6.4.1 Conclusion

Social networks provide a useful tool for exploring social interactions in groups and in this chapter, I have shown its application to exploring *Sapajus-Saimiri* single- and mixed-species networks, in relation to their "groupness". It is clear from the analyses that both the West and East *Sapajus* and *Saimiri* were behaving as separate groups, providing a valuable contribution to our current understanding (or misunderstanding) of mixed-species groups. The next steps for future research will be to explore more in-depth analyses such as multi-layer networks (e.g. Finn, Silk, Porter & Pinter-Wollman, 2019; Pereira, Rebelo, Cassanova, Lee & Louca, 2020), to integrate various types of interactions (e.g. affiliative, neutral, antagonistic) in relation to proximity, and their dynamics in a network structure in order to better understand individual roles within their social relationships of mixed-species groups.

7 GENERAL DISCUSSION

Separate discussion sections have been provided at the end of each data Chapter, and so in this discussion I will reiterate the salient points that were described and will relate them back to the study aims outlined in Chapter 1. In particular I discuss the findings with respect to enclosure design, and the impact that this may have on “groupness” in captivity, as well as the more theoretical and methodological contributions of my research findings.

7.1 Synopsis

Revisiting the main aim outlined in Chapter 1, rather than attempting to create an all-encompassing definition of mixed-species groups, I instead set out to develop, and test a more operational definition that is more considerate of the diversity and complexity in which animals live. While I do not totally agree with previous attempts at definitions (due to either their ambiguity or not being applicable across different animal societies), there are still elements that can be used as part of an overall framework such as: 1) group stability; 2) an element of socialness (i.e. interactions); 3) proximity and behavioural coordination in time and space, and 4) a minimum of two individuals co-present in an environment. Stability and socialness were examined in Chapter 6 using social network analyses, and proximity and coordination in time and space were examined in two parts; proximity in time and space was examined in Chapter 4 through the monkey’s space use, and coordination in time and space was examined in Chapter 5 using behavioural synchrony (see also Figure 1.1). Previous research on mixed-species groups (depending on the species involved) have often been described as varying in their duration (e.g. minutes, hours, years), frequency (e.g. daily, seasonally) and structure, with individuals frequently joining and leaving (see Cords, 1987). Furthermore, proximity measures used to define whether different species were observed as a mixed-species group are often based on arbitrary distances (e.g. <20m, <50m or 100yds) or descriptions of feeding in the same tree (e.g. Struhsaker, 1981). My studies highlight the exciting possibilities of methodological approaches where it is possible to quantify 'groupness' (see section 7.3).

7.2 Overlap in time and space

Chapters 2 and 4 provide my findings on *Sapajus-Saimiri*'s use of space, which relates to one of the four prerequisites of grouping (3 proximity in time and space). It was important for me to undertake fieldwork in order to better understand the behavioural ecology of my study species in their natural habitats. While I was originally planning on conducting the entirety of my fieldwork at the Raleighvallen field site (primary forest), by also collecting data at Peperpot (secondary forest) I was able to gain some useful insights into the differences in my study species behaviours and use of space (i.e. vertical and horizontal spread). This highlighted the variability and the influence of the environment on grouping patterns. Therefore, it must be acknowledged that while the potential is there for *Sapajus* and *Saimiri* to form mixed-species groups, this does not necessarily mean that they will always form mixed-species groups when observed together, and may instead be behaving more as an association or aggregating around a resource (see Figures, 7.1, 7.2 and 7.3). Unfortunately, due to the low encounter rates (and not being able to identify specific individuals) at both field sites it was not possible to make any inferences about the stability of the groups observed.

Having conducted fieldwork as part of this thesis, I can better appreciate why previous studies used arbitrary distances (e.g. <20m, <50m or 100yds) as measures of proximity between different species; especially for arboreal species living in dense forests. However, I still believe that proximal distances alone are not sufficient when postulating that two or more species within a certain distance are forming a mixed-species group (i.e. no real difference to an association or aggregation). As has been discussed extensively throughout this thesis, foraging advantages and reduced risk of predation are the two main driving factors selecting for mixed-species groups. This is why for my fieldwork I collected measures of group spread (i.e. the maximum vertical and horizontal distance of the observable group – see Chapter 2) to examine if they were vertically and horizontally co-present in time and space, in conjunction with their activities; specifically foraging and vigilance. By noting the maximum observed distances (vertical and horizontal) of the group as a whole (i.e. group spread – see Smith, Buchanan-Smith, Surridge & Mundy, 2005) and the minimum interspecific distances between the different species, it is possible to move beyond arbitrary measures in relation to quantifying spatial proximity. Furthermore, by also collecting data on the frequency of foraging and vigilance observed during single-species and mixed-species observations, it is possible to examine whether there is a difference as a result of mixing (i.e. increased foraging and reduced vigilance). In other words, we can quantify the extent to which the different species are overlapping in time and space in conjunction with the double benefits of grouping.

In captivity it is possible to test group spread in a more controlled and constrained (i.e. smaller compared to the wild) environment, applying the same methods as noted above. However, it is also possible to focus on specific areas and/or substrates of interest within an enclosure (e.g. meaningful zones - see Chapter 4) in relation to overlap between species in time and space. Based on the findings in Chapter 4, we know that while there was some vertical overlap in space use by *Sapajus* and *Saimiri*, they did not overlap as much horizontally (i.e. using different areas), especially in their shared outdoor enclosure, and there was also very little overlap in time (i.e. in different areas and heights during a scan). Overall, these differences in use of space (and in time) indicate that the monkeys were not socially attracted to the presence of the other, and therefore should not be described as a mixed-species group (see Table 7.2). However, given that in the wild *Sapajus* and *Saimiri* have much larger home ranges, allowing them to be spread out across distances that are larger than in captivity, perhaps overlap within specific zones in shared enclosures is not as essential, as they would still be co-present in the overall space (i.e. in the same enclosure at the same time). Furthermore, even though *Sapajus* and *Saimiri* may be more spatially separated in the wild than in captivity, generally there are enough connecting substrates to allow both species to travel and mix, suggesting it is not environmental constraints in the wild that limit mixing. For example, in most habitats if there were any gaps between the trees then the monkeys were able to jump and leap between them (personal observations in Suriname). At Living Links there is less connectivity between zones that would allow for arboreal movement, which resulted in the monkeys either having to traverse along the ground or to stay in zones that were better suited to their spatial needs. For instance, in the shared outdoor enclosure, *Sapajus* were most frequently observed in zones that had large vertical structures (i.e. mimicking low-mid levels of the canopy in the wild) and *Saimiri* in zones that had bushes, which mimic the forest understory (see Chapter 4).

It is possible that providing more off the ground connectors between zones and substrates that suit both species could provide more opportunities for the monkeys to overlap in their space use as a true mixed-species group. Indeed, the results from Chapter 2 and 4 have already been used to provide recommendations for a refurbishment of the outdoor shared enclosure at Living Links (see Appendix VIII), as part of the long-term 'Living Together' project. However, preliminary findings indicate that there is still little overlap in time and space use between the species, with the majority of new substrates being used more frequently by *Sapajus* (see Appendix IX). However, the lack of overlap observed post refurbishment may be due to the time of year in which the data were collected (winter/early spring; outdoor enclosure use increases in warmer temperatures), and observation times being limited to the opening hours of the zoo (i.e. does not account for every hour of the day 24/7 approach – see Brando & Buchanan-Smith, 2018). Alternatively, the lack of overlap could simply be due to the captive environment not providing the conditions (i.e. double benefits of grouping – see Chapter 1) that select for mixed-species groups in the wild. In captivity, food is provided regularly and there is little to no risk of predation, and if foraging advantages and reduced risk of predation are necessary for different species to form mixed-species groups then perhaps it is not as surprising that *Sapajus* and *Saimiri* are behaving more as two separate groups sharing an exhibit.

Examining group spread allows researchers to measure and quantify groupness in terms of more general proximity in time and space. However, as mentioned previously (see Chapter 1) group-living animals often live in complex societies, and while the study of space use provides a good starting point for quantifying groupness in mixed-species groups, it does not consider the socialness of animals. Therefore, if animals in captivity are observed to be behaving as true mixed-species groups irrespective of the double benefits of grouping, then there must be some other explanation, such as cognitive social benefits, whereby the presence of the other species could be more socially stimulating, providing opportunities for play, and interacting with others (e.g. Daoudi, Badihi & Buchanan-Smith, 2017). Therefore, other methods of measuring the more social elements of groupness (i.e. coordination in time and space, group stability and interactions) are required.

7.3 Socialness, group stability & coordination in time & space

How different species behave and interact with each other in time and space can provide useful measures for quantifying groupness in mixed-species groups. Chapter 5 examined groupness in relation to behavioural coordination in time and space, by investigating behavioural synchrony at the group-level. Chapter 6 examined group stability and the interactions (e.g. using proximity as a proxy measure) between individuals, using social network analyses.

As mentioned in the above sections *Sapajus* and *Saimiri* were not found to overlap much in their use of the shared outdoor enclosure (see also Chapter 4), however they were still within close enough proximity for communication and information exchange to occur (e.g. visual and vocal cues – see Chapter 1). One of the prerequisites for group-living is for individuals to be coordinated in time and space. This can be problematic when considering single-species groups due to the differences in age/sex classes, social and reproductive interests and strategies, and physiological and metabolic needs (see Chapter 1), which can present further issues when including another species. However, when considering that foraging advantages and reduced risk of predation are the main selective drivers for grouping, then it would be in the best interest of individuals (in terms of fitness) that they remain coordinated with other group members. Behavioural synchrony is one way to measure and quantify the coordination of mixed-species groups (see Figure 7.4), and while the methods used to examine behavioural synchrony (e.g. scan sampling, Simpson's diversity index) was not new, the examination of the data from multiple perspectives (e.g. descriptives, linear models and correlation matrices) allowed for some insightful observations between various levels of explanation. The behavioural synchrony seen among individuals in single-species groups indicate that the measure is methodologically sound, however, no such synchrony was found between members of the different species. Yet the findings are informative for species management, for example, knowing that the proportion of *Sapajus* present and the location of individuals influence behavioural synchrony in mixed-groups, can highlight potential welfare concerns (e.g. if one species are avoiding coming into contact with the other). However, as noted above the results are taken from data collected during the summer months and during zoo opening hours, which leaves ~16 hours of the day and nine months of the year unaccounted for. Furthermore, the use of scan methods may have meant that some behaviours and individuals were missed, meaning that the results are not entirely representative of the groups. Future research efforts may wish to use a combination of focal and scan data to examine synchrony at both the individual and group level and monitor the groups 24/7 throughout the year (Brando & Buchanan-Smith, 2018).

Similarly social network analysis (SNA) has been noted as a powerful and comprehensive tool for investigating and quantifying the stability and dynamics of social relationships, but it typically focusses on a single type of interaction (e.g. grooming [Kanngiesser, Sueur, Riedl, Grossmann & Call, 2011]; aggression [Crofoot, Rubenstein, Maiya & Berger-Wolf, 2011], proximity [Zhang et al., 2012]), or compares the results across networks derived from several behaviours (e.g. Lehmann & Ross, 2011), which is often viewed as a limitation because interactions between individuals vary temporally and spatially and can occur across many social contexts (i.e. affiliative, neutral, agonistic). Therefore, the multidimensionality of relationships can often be missed when focussing on only one aspect at a time (i.e. how does each type of interaction contribute to the overall result). Despite these limitations, I believe that SNA was appropriate for this exploratory investigation of mixed-species primate social networks, demonstrating a very clear pattern using proximity alone. Nevertheless, future studies may want to consider exploring more in-depth analyses such as multi-layer networks (see Figure 7.4), to better understand individual roles within their social environment (e.g. Finn, Silk, Porter & Pinter-Wollman, 2019; Pereira, Rebelo, Cassanova, Lee & Louca, 2020).

Finally, it must be noted that it would be difficult (though not impossible) to apply the above-mentioned methods in the field. Although it would be possible to examine, behavioural synchrony and social networks in environments that are more open and where it is generally easier to view study subjects (e.g. savannah), it would be more problematic in environments of dense vegetation with unhabituated groups. However, this could be viewed as an exciting opportunity to further develop and refine the methods in captivity so that they can be tested in different field conditions.

7.3 Welfare implications

Animal welfare is notoriously difficult to measure, and as such it generally requires a multifaceted approach, with links to animal health (e.g. physiological and biochemical measures) and behaviour (e.g. stereotypies - repetitive, unvarying, and seemingly functionless behaviour patterns), in order to gain a more complete picture (see Ödberg, 1978; Mason, 1991; Mason & Latham, 2004; Bassett & Buchanan-Smith, 2007; Mellor, 2016; Appleby et al., 2018). The best-known examples of criteria used to assess whether an animal is experiencing good or bad welfare are taken from the Five Freedoms (see FAWC, 1979), the Five Provisions (see Mellor & Reid, 1994), and more recently the Five Domains Model (see Mellor, 2016). In relation to the studies in this thesis (i.e. using a combined captive-field approach to research) the criteria that I deemed to be most relevant to my research are outlined in Table 7.1.

Table 7.1 *An abbreviated version of the Five Freedoms, Five Provisions and Five Domains that relate specifically to the combined captive-field approach to space use, behavioural synchrony, and social networks in* Sapajus-Saimiri *mixed-species groups.*

Model	**Criteria**	**Author(s)**
Freedom	***Fifth freedom*** Freedom to express normal behaviour	FAWC, 1979
Provision	***Fifth provision*** By providing sufficient space, proper facilities, and company of the animal's own kind	Mellor & Reid, 1994
Domain	***Survival-related factors*** (2) Environment *Positive*: physical environment comfortable or pleasant *Negative*: uncomfortable or unpleasant physical features of environment ***Situation-related factors*** (4) Behaviour *Positive*: able to express rewarding behaviours *Negative*: behavioural expression restricted	Mellor, 2016

Most modern zoos have five interconnected goals which are (1) welfare, (2) conservation, (3) education of the public, (4) research and (5) entertainment (see Hosey, 2005; AZA, 2008; Rees, 2011; Bowler, Buchanan-Smith & Whiten, 2012 – see also Chapter 2, Section 2.2.1). For many zoos there is a major emphasis on the first four goals, however, for the most part zoo visitors will come for the purpose of entertainment (e.g. Altman, 1998; Reade & Waran, 1996; Fernandez, Tamborski, Pickens & Timberlake, 2009). Thus, without attracting and entertaining visitors, zoos would likely struggle to achieve (and maintain) their other goals. One way that zoos are able to meet these goals is by designing more naturalistic enclosures, which can not only improve the welfare of animals (i.e. more likely to engage in normal and rewarding behaviours), but can also be of benefit to researchers (i.e. improved ecological validity), in addition to educating the public as well as providing entertainment, which can in turn aid with conservation goals (e.g. fundraising for projects) (Reade & Waran, 1996; Hosey, 2005; AZA, 2008; Fernandez et al., 2009; Rees, 2011; Bowler et al., 2012; Mellor, 2016).

Captive animals are invariably held in an environment that is much smaller and less complex than their natural habitat (e.g. Chamove & Anderson, 1989; Buchanan-Smith, 1997). However, animals that are housed in mixed-species exhibits are generally more likely to be in larger enclosures than animals in single-species exhibits, with the hope that it will facilitate more naturalistic (species-specific) behaviours (e.g. leaping and jumping in arboreal primates), that can be more directly compared with wild observations. Larger naturalistic enclosures can also facilitate increases in social complexity, cognitive challenges, and reduced stereotyped and stress-related behaviour, which can all lead to improved welfare (Thomas & Maruska, 1996; Buchanan-Smith, 1999b; Buchanan-Smith et al., 2004, 2013; Prescott & Buchanan-Smith, 2004; Dalton & Buchanan-Smith, 2005; Heymann, Sicchar Valdez, & Tapia, 1996; Leonardi et al., 2010), whilst simultaneously providing a more entertaining and informative experience for zoo visitors (e.g. Bowler et al., 2012). However, it must be noted that while it is important for animals to have adequate space in which there are opportunities to display their full set of behavioural repertoires, studies have also shown that quality of space is equally important (Paulk, Dienske, & Ribbens, 1977; Ogden, Finlay & Maple,1990; Kerl & Rothe, 1996; Buchanan-Smith et al., 2004; Estevez & Christman, 2006; Ross & Lukas, 2006; Ross, Schapiro, Hau, & Lukas, 2009). Large naturalistic enclosures may look appealing to zoo visitors but may be of limited value to the animals if they are unable to make use of all the space available or compete for space. For instance, Leonardi et al. (2010) found that initially when the monkeys were moved to Living Links there were more instances of aggression around specific substrate/enclosure furnishings and once these were addressed with a refurbishment, instances of aggression reduced. Furthermore, Buchanan-Smith et al. (2013) note that deterioration and/or changes to enclosures can also impact on other research that takes place at Living Links (i.e. cubicle research).

In addition to benefitting from being housed in larger naturalistic enclosures (i.e. more opportunities for environmental enrichment such as natural foraging), housing species together in a mixed-species exhibit can provide a form of social enrichment (as long as the species naturally associate in the wild - see Sodaro, 1999; Leonardi et al., 2010; Buchanan-Smith, 2012; Buchanan-Smith et al., 2013; Daoudi et al., 2017). However, as there have been varying degrees of success in housing multiple species in an exhibit, it is important that groups are monitored carefully, not only via their use of space, but also by examining their behaviour(s) and their patterns and quality of interactions with both conspecifics and heterospecifics. By combining different methodological approaches for longitudinal studies such as the ‘Living Together’ project at Living Links, we can gain more detailed knowledge on the social stability of groups in captivity, and for mixed-species groups this will help to ensure that sharing an exhibit is not detrimental to the welfare of the animals.

7.3 Methodological and theoretical contributions

The strongest methodological contribution of this thesis is developing and testing quantifiable prerequisites for “groupness”, of both single-species and mixed-species groups. The findings clearly illustrate that the single-species groups housed in Living Links met these prerequisites. However, when considering the clear separation between *Sapajus* and *Saimiri* in the mixed-species social networks, along with the lack of horizontal overlap in the monkey’s space use in shared enclosures (Chapter 4), and the asynchronicity of their behaviours in mixed-species groups (Chapter 5), it is evident that they are not behaving as true mixed-species groups (see Table 7.2). Additionally, there were clear differences between the West and East groups. For instance the results for the East group indicate that they can be described more as a mixed-species association (see Figure 7.2), whereas the West group were behaving more as two separate groups who happen to co-exist in a mixed-species exhibit (see Table 7.2), and cannot even really be described as an aggregation (see Figure 7.3). This variability could be due to the differences in group dynamics (i.e. a much smaller number of *Saimiri* in the West group, or East *Sapajus* more tolerant of *Saimiri*), but perhaps it may be due to differences in individual preferences (see Coleman, 2012).

Table 7.2 *Variability in the groupness of the West and East groups at Living Links (see also Figures 7.1-7.3).*

West	East
Overlap in time and space (Chapter 4)	
co-present 34% of scans (*n*=90).	co-present 84% of scans (*n*=90).
Some vertical separation, *Sapajus* observed more at heights >2m compared to *Saimiri*, but both species spent a high proportion of observations >2m and on the ground.	Some vertical separation, *Sapajus* observed more at heights >2m compared to *Saimiri*, but both species spent a high proportion of observations >2m and on the ground.
Overall *Sapajus* were using more of the outdoor space compared to *Saimiri. Sapajus* were observed for a higher proportion of scans in central zones of the outdoor enclosure, while *Saimiri* were more on the periphery.	Overall *Sapajus* were using more of the outdoor space compared to *Saimiri.* But the difference is not as extreme as with the West group. *Sapajus* were observed for a higher proportion of scans in central zones of the outdoor enclosure, while *Saimiri* were more on the periphery.
No evidence of social attraction.	Some evidence of social attraction.
Coordination in time and space (Chapter 5)	
Low proportion of scans where *Saimiri* were observed in shared enclosures (*Sapajus* indoor = 0.03*, outdoor = 0.21).	High proportion of observations where *Saimiri* were observed in shared enclosures (*Sapajus* indoor = 0.69, outdoor = 0.69).
Behavioural synchrony in *Saimiri* was significantly higher in the shared outdoor enclosure compared with their own indoor enclosure (*too few data to examine when observed in *Sapajus* indoor enclosure).	Behavioural synchrony in *Saimiri* was significantly higher in shared enclosures (*Sapajus* indoor and outdoor) compared with their own indoor enclosure.
There was no significant difference in behavioural synchrony in *Sapajus* when in their indoor enclosure or the shared outdoor enclosure.	There was no significant difference in behavioural synchrony in *Sapajus* when in their indoor enclosure or the shared outdoor enclosure.
Evidence for single-species synchrony, but not for mixed-species.	Evidence for single-species synchrony, but not for mixed-species.
Stability, socialness and overlap in time and space (Chapter 6)	
Mixed-species social networks indicate that network position was determined by species: *Sapajus* were more central than *Saimiri*.	Mixed-species social networks indicate that network position was determined by species: *Sapajus* were more central than *Saimiri*.
Distinctly two separate clusters with few ties between species.	Distinctly two separate clusters with some ties between species.
Little evidence for socialness or overlap in time and space between species.	Little evidence for socialness or overlap in time and space between species.
Groupness	
Results of the three studies indicate that the West group are two separate groups coexisting in a mixed exhibit.	Results of the three studies indicate that the East group are a mixed-species association at least some of the time, rather than a mixed-species group or aggregation.

Another possible explanation for why the monkeys were not behaving as true mixed-species groups (as mentioned above) could be that within the captive environment the factors that would typically select for mixed-species groupings in the wild (i.e. foraging advantages and reduced risk of predation) are not necessary (i.e. constant food supply and little to no risk of predation). Therefore, if conditions in captivity allow for the monkeys to have better overlap in time and space (i.e. appropriate substrates that allow both species to move between all zones), and perhaps enrichment activities that facilitate the double benefits of grouping, then the monkeys may be more likely to behave as a true mixed-species group. Though whether this is desirable for their welfare is debateable, as forcing them to come into proximity may cause stress to one or both species, and/or incite aggression through competition of resources. Thus, it is important to consider enclosure design and enrichment activities carefully, so that while they may better facilitate the two species to mix, it is not to the detriment of their welfare (i.e. the monkeys have the option to choose whether they want to come into proximity or not).

Furthermore, this thesis has highlighted the importance and relevance of fieldwork when studying animals in captivity (i.e. combined captive-field approach to research). While the captive environment does allow the testing of hypotheses in a controlled environment, if the conditions (i.e. enclosure design, species combinations etc) are not representative of that in the wild, then the ecological validity of the research being undertaken may be called into question. It was for this reason that an additional aim of this field research was to look towards re-establishing a field station at the Raleighvallen Nature Reserve, in order to study the groups in more detail as part of a longitudinal project that is linked to the 'Living Together' project at the Living Links. The Raleighvallen Nature Reserve should be considered as a viable location for a long-term field site, that can be connected to Living Links: (1) the correct species are present; (2) accommodation is available (via Conservation International, Suriname); (3) the site is relatively easy to access (1 day travel compared to 3-day travel to the Cocha Cashu field site in Peru); (4) enable conservation, ecological and behavioural research in situ and (5) inform enclosure design to improve welfare in captivity.

Finally, as a result of my findings in this thesis I propose the following operational definitions that are in line with the four prerequisites of grouping:

(1) **mixed-species group:** there needs to be at least one individual of two or more species co-present within an environment, individuals need to overlap and be synchronous in time and space, and have multiple and strong ties (i.e. repeated contacts and social attraction) between individuals of the different species (see Figure 7.1);

(2) **mixed-species association:** there needs to be at least one individual of two or more species gathering together (i.e. due to social attraction), but not due to key resources (e.g. food or watering hole), individuals need to overlap in time and space use, at least temporarily, and may possibly be synchronous (but not as a prerequisite) due to being gathered together, and there may be interactions and repeated contacts, though these are not prerequisites for association (see Figure 7.2);

(3) **aggregation:** there needs to be at least one individual of two or more species using the same resource, individuals will overlap in time and space, at least temporarily due to aggregating around a resource, and may possibly be synchronous in their activities (e.g. drinking if at a watering hole), interactions and stability of repeated contacts are not prerequisites as individuals are gathered together due to a resource rather than due to social attraction (see Figure 7.3).

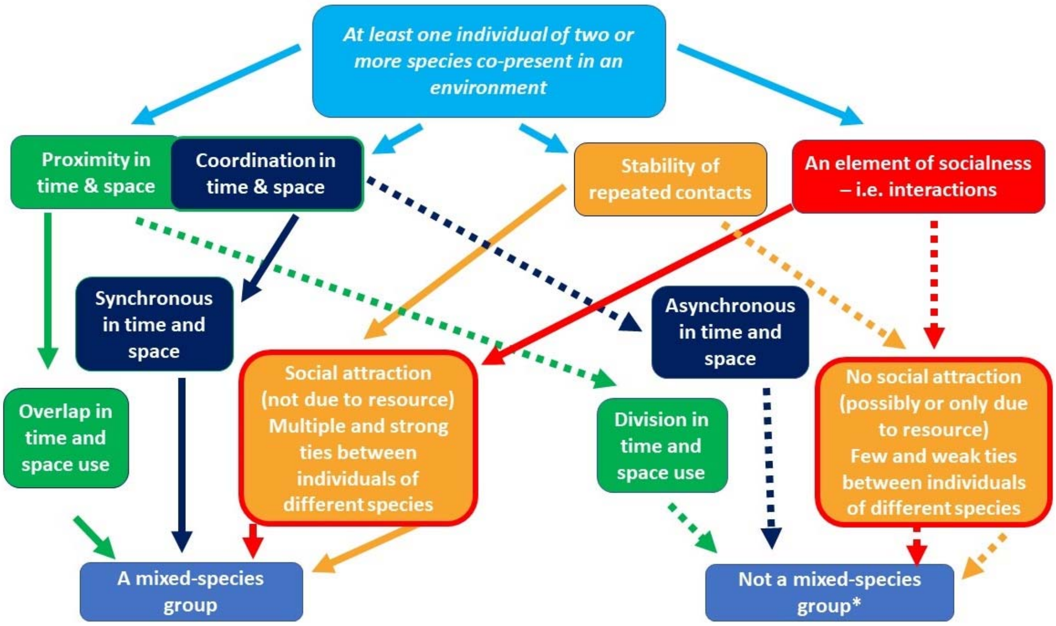


Figure 7.1 Schematic illustration of the prerequisites for mixed-species groups. If not a mixed-species group then could be *an association (see Figure 7.2) or aggregation (see Figure 7.3). Individuals of different species must be independent (i.e. moving separately rather than on or inside each other).

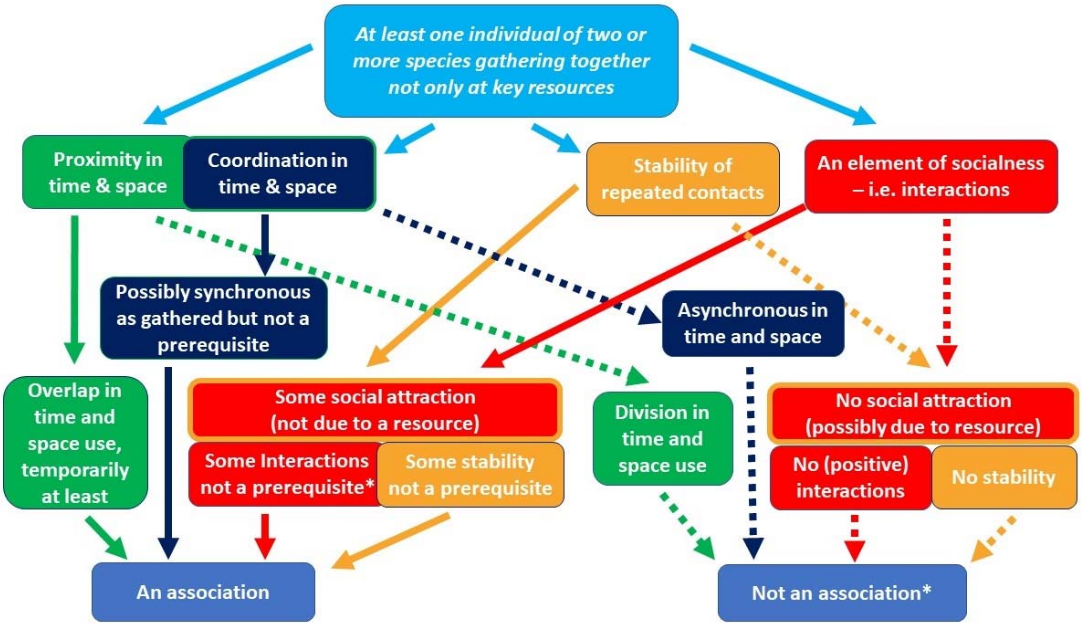


Figure 7. 2 Schematic illustration of the prerequisites for mixed-species associations. If not a mixed-species association then could be *an aggregation (see Figure 7.3). Individuals of different species must be independent (i.e. moving separately rather than on or inside each other).

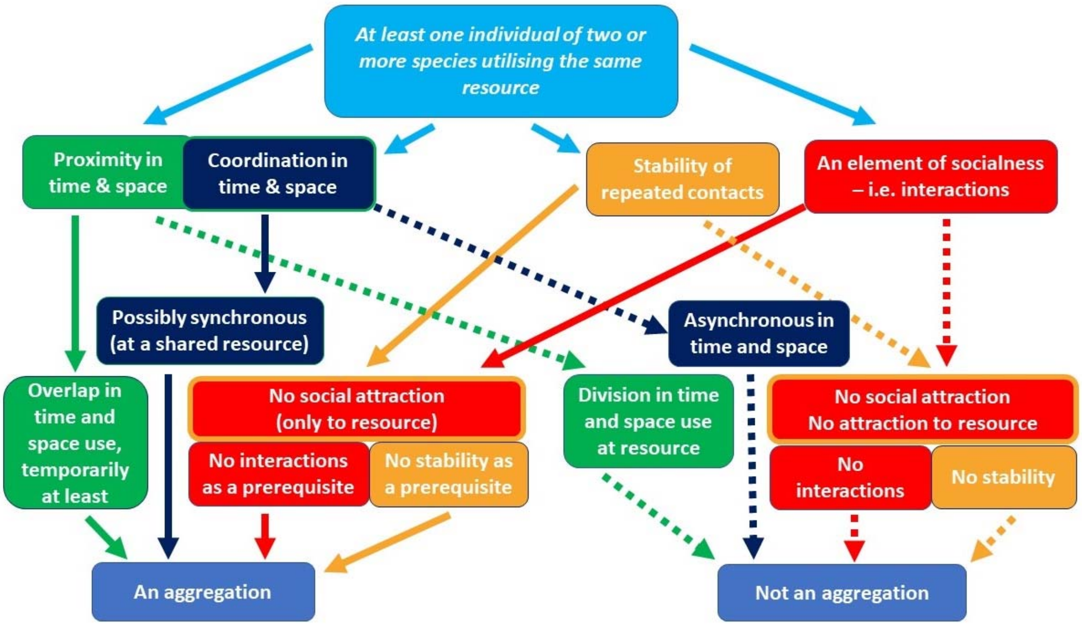


Figure 7.3 Schematic illustration of the prerequisites for mixed-species aggregations. Individuals of different species must be independent (i.e. moving separately rather than on or inside each other).

7.4 Conclusions

My goal was not to provide a sterile list of criteria that former definitions of mixed-species groups have provided which do not consider their social complexity. I do not claim that studies would need to adopt all of the methods mentioned in this thesis in order to determine whether two or more species can be considered a mixed-species group. However, I would argue that combining the three prerequisites with group stability as the key factor that distinguishes between a mixed-species group an association and an aggregation (see Figures 7.1, 7.2 and 7.3), will provide a more thorough understanding of groupness. For instance overlap in time and space alone could be either a mixed-species group or mixed-species association or even an aggregation (see Figures 7.1, 7.2 and 7.3), and so studying coordination (e.g. behavioural synchrony) in time and space is also needed. Furthermore, an element of socialness via direct and/or indirect interactions (including vocal communication) and social attraction is also required so as to distinguish groups and associations from an aggregation. Therefore, unlike the previous definitions for mixed-species groups mentioned in Chapter 1 (e.g. Stensland, Anderbjörn & Berggren, 2003; Goodale, Beauchamp & Ruxton, 2017 - see also Section 1.4), my operational definitions allow for more complex societies such as fission-fusion communities in addition to temporary parent-infant units to be considered groups.

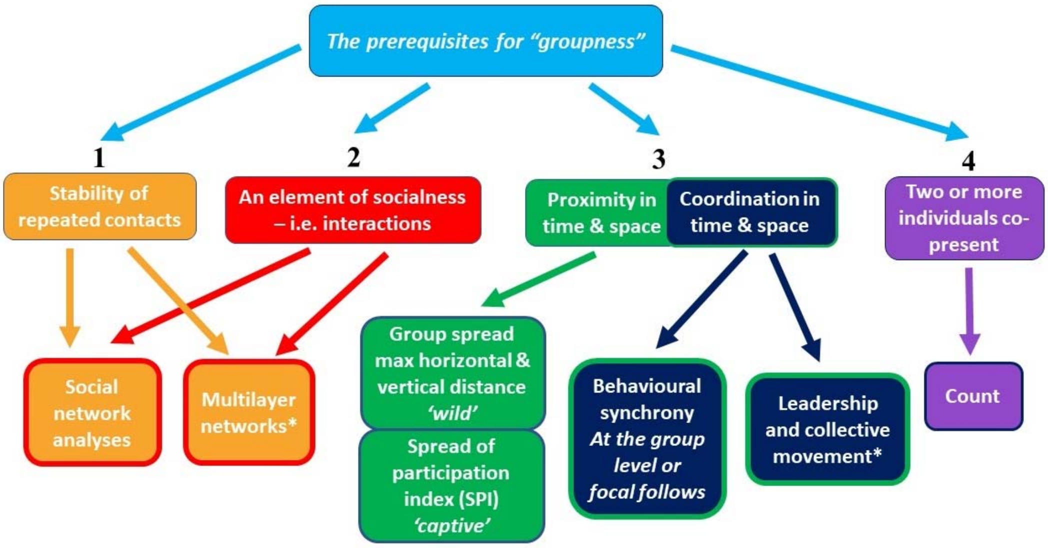


Figure 7. 4 Schematic illustration of the prerequisites and methodological approaches to quantifying the groupness of mixed-species groups (*methods that could be used in future research).

Researchers wanting to gain more of an understanding of the behaviour and nature of mixed-species groups (i.e. which individuals/species are maintaining them, interact more and benefit more) should consider using a combination of different methodological approaches, such as those outlined in Figure 7.4. I have suggested that multilayer networks could be used in order to test prerequisites 1 and 2, as mentioned above (Section 7.3), there are limitations to solely using social network analyses, and multi-layer networks will allow for more in-depth analyses of individuals and their roles within their social environment(s). Furthermore, I suggest that in order to further examine coordination in time and space, researchers could also look at leadership and collective behaviour in mixed-species groups (see Figure 7.4), as even at the group-level, decision making regarding collective group movement(s) almost always involves some form of leadership (e.g. Rasa, 1987; Stewart & Harcourt, 1994; Boinski & Garber, 2000; Dyer, Johansson, Helbing, Couzin & Krause, 2009; King, Johnson & van Vugt, 2009; Fitchel, Pyritz & Kappeler, 2011; van Belle, Estrada & Garber, 2013). Studies that are able to quantify the contribution of individuals to group stability and coordination (in time and space) will provide critical insights into the behavioural mechanisms underlying the formation and maintenance of mixed-species groups.

By developing and testing a framework of groupness, my research has demonstrated the fluidity of mixed-species groups, associations, and aggregations both in the wild and captivity. For instance, the same two species coexisting in two different areas (e.g. wild: Raleighvallen and Peperpot or captive: West and East exhibits at Living Links) may or may not form mixed-species groups, which could be dependent on a range of factors, such as those that are directly linked to the double benefits of grouping (e.g. the environment and available resources, predation risk), as well as group size and individual differences. As a result of my findings, I have provided clearer operational definitions that can be applied to test the groupness of mixed-species animal groupings.

8 REFERENCES

Agetsuma, N. (1995). Foraging synchrony in a group of Yakushima macaques (*Macaca fuscata yakui*). *Folia Primatologica, 64*, 167-179.

Alberts, S. C. (1994). Vigilance in young baboons: effects of habitat, age, sex and maternal rank on glance rate. *Animal Behaviour*, *47*, 749-755.

Alberts, S. C., Altmann, J., & Wilson, M. L. (1996). Mate guarding constrains foraging activity of male baboons. *Animal Behaviour, 51*, 1269-1277.

Alexander, R. (1974). The evolution of social behaviour. *Annual Review of Ecology and Systematics, 5*, 325-383.

Altmann, J. (1974a). Observational study of behavior-sampling methods. *Behaviour, 49*, 227-267.

Altmann, J. (1980). *Baboon mothers and infants*. Harvard University Press.

Altman, J. D. (1998). Animal activity and visitor learning at the zoo. *Anthrozoös, 11*, 12-21.

Altmann, S. A. (1974b). Baboons, space, time, and energy. *American Zoologist*, *14,* 221-248.

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology*, *18*, 1415-1419.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 4199-4205.

Appleby, M., Coleman, G., Olsson, A., Galindo, F., Bennett, R., Blache, D., Boissy, A., Burn, C. C., Butterworth, A., & Cockram, M. (2018). *Animal Welfare* (pp. 35-64). CAB International.

Arenz, C. L., & Leger, D. W. (2000). Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. *Animal Behaviour*, *59*, 535-541.

ASAB. (2012). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour*, *83*, 301–309.

Association of Zoos and Aquariums (AZA). (2008). AZA Mission Statement. Retrieved online: http://www.aza.org/AboutAZA/mission/index.html.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B., & van Schaik, C. P. (2008). Fission-fusion dynamics: new research frameworks. *Current Anthropology*, *49*, 627-654.

Baal, F. L., Mittermeier, R. A., & van Roosmalen, M. G. (1988). Primates and protected areas in Suriname. *Oryx, 22*, 7-14.

Badihi, I. (2006). The effects of complexity, choice and control on the behaviour and the welfare of captive common marmosets (*Callithrix jacchus*) [Unpublished doctoral thesis]. The University of Stirling, Scotland.

Baker, A. J., Dietz, J. M., & Kleiman, D. G. (1993). Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Animal Behaviour, 46*, 1091-1103.

Baker, K. C. (1997). Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association*, *16*, 225-236.

Baker, K. C., & Aureli, F. (1997). Behavioural indicators of anxiety: An empirical test in chimpanzees. *Behaviour, 134*, 1031-1050.

Baldwin, J. D. (1968). The social behavior of adult male squirrel monkeys (*Saimiri sciureus*) in a seminatural environment. *Folia Primatologica, 9,* 281-314.

Baldwin, J. D. (1985). The behavior of squirrel monkeys (*Saimiri*) in natural environments. In: L.A. Rosenblum, C.L. Coe, (Eds.). *Handbook of squirrel monkey research* (p 35–53). Plenum Press.

Baldwin, J. D., & Baldwin, J. I. (1971). Squirrel monkeys (*Saimiri*) in natural habitats in Panama, Colombia, Brazil, and Peru. *Primates, 12*, 45-61.

Baldwin, J. D., & Baldwin, J. I. (1981). The squirrel monkeys, genus *Saimiri. In:* A.F. Coimbra-Filho, & R.A. Mittermeier, (Eds.). *Ecology and behavior of neotropical primates. Academia Brasileira.*

Barbour, M. G., Burk, J. H., & Pitts, W. D. (1987). *Terrestrial plant ecology (2nd ed.).* Benjamin Cummings.

Barnard, C. J. (1983). *Animal behaviour: ecology and evolution.* Croom Helm.

Barrett, L., Halliday, J., & Henzi, S. P. (2006). The ecology of motherhood: the structuring of lactation costs by chacma baboons. *Journal of Animal Ecology, 75,* 875-886.

Bartecki, U., & Heymann, E. W. (1987). Field observation of snake-mobbing in a group of saddle-back tamarins, *Saguinus fuscicollis nigrifrons. Folia Primatologica, 48,* 199-202.

Bassett, L., & Buchanan-Smith, H. M. (2007). Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science, 102*, 223-245.

Bayly, K. L., Evans, C. S., & Taylor, A. (2006). Measuring social structure: a comparison of eight dominance indices. *Behavioural Processes, 73*, 1-12.

Beauchamp, G. (2006). Spatial, temporal and weather factors influencing the foraging behavior of migrating Semipalmated Sandpipers. *Waterbirds, 29*, 221-225.

Beauchamp, G. (2009). Sleeping gulls monitor the vigilance behaviour of their neighbours. *Biology Letters, 5*, 9–11.

Bednekoff, P. A., & Lima, S. L. (1998). Randomness, chaos and confusion in the study of antipredator vigilance. *Trends in Ecology & Evolution, 13,* 284-287.

Beekman, M., & Ratnieks, F. L. W. (2000). Long-range foraging by the honey-bee, *Apis mellifera* L. *Functional Ecology*, *14*, 490-496.

Bejder, L., Fletcher, D., & Bräger, S. (1998). A method for testing association patterns of social animals. *Animal behaviour, 56*, 719-725.

Bell, R. (1971). A grazing ecosystem in the serengeti. *Scientific American, 225,* 86-93.

Bercovitch, F. B. (1992). Estradiol concentrations, fat deposits, and reproductive strategies in male rhesus macaques. *Hormones and Behavior, 26*, 272-282.

Bergman, T. J., & Beehner, J. C. (2015). Measuring social complexity. *Animal Behaviour, 103,* 203-209.

Berman, C. M., Rasmussen, K. L. R., & Suomi, S. J. (1997). Group size, infant development and social networks in free-ranging rhesus monkeys. *Animal Behaviour, 53*, 405-421.

Bernstein, I. S. (1967). Intertaxa interactions in a Malayan primate community. *Folia Primatologica, 7*, 198-207.

Bernstein, I. S. (1981). Dominance: the baby and the bathwater. *The Behavioral and Brain Sciences, 4*, 419-457.

Berry, P. E., Huber, O. & Holst, B. K. (1995). Floristic analysis and phytogeography. In: Berry, P.E., Holst, B.K. & Yatskievych, K. (eds.) *Flora of the Venezuelan Guayana, Vol. 1. Introduction* (pp. 161–191). Missouri Botanical Garden Press.

Bertram, B. C. R. (1978). Living in groups: predators and prey. In J.R. Krebs & N.B. Davies (Eds.) *Behavioural Ecology* (pp. 64-96). Blackwell Scientific.

Bertram, B. C. R. (1980). Vigilance and group size in ostriches. *Animal Behaviour, 28*, 278–286.

Beyer, K., Gozlan, R. E., & Copp, G. H. (2010). Social network properties within a fish assemblage invaded by non-native sunbleak *Leucaspius delineatus*. *Ecological Modelling, 221,* 2118-2122.

Blake, S. (2002). The ecology of forest elephant distribution and its implications for conservation [Unpublished doctoral thesis]. The University of Edinburgh, Scotland.

Blake, S., & Inkamba-Nkulu, C. (2004). Fruit, minerals, and forest elephant trails: do all roads lead to Rome? *Biotropica*, *36*, 392-401.

Boccaletti, S., Bianconi, G., Criado, R., Del Genio, C. I., Gómez-Gardenes, J., Romance, M., Sendiña-Nadal, I., Wang, Z., & Zanin, M. (2014). The structure and dynamics of multilayer networks. *Physics Reports*, *544*, 1-122.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford University Press.

Boinski, S. (1987a). Mating patterns in squirrel monkeys: Implications for seasonal sexual dimorphism. *Behavioral Ecology and Sociobiology, 21,* 13–21.

Boinski, S. (1987b). Birth synchrony in squirrel monkeys (*Saimiri oerstedi*). *Behavioral Ecology and Sociobiology, 21,* 393-400.

Boinski, S. (1988a). Sex differences in the foraging behaviour of squirrel monkeys in a seasonal habitat. *Behavioural Ecology and Sociobiology, 23,* 177-186.

Boinski, S. (1988b). Use of a club by a wild white-faced capuchin (*Cebus capucinus*) to attack a venomous snake (*Bothrops asper*). *American Journal of Primatology*, *14*, 177-179.

Boinski, S. (1989). Why don't *Saimiri oerstedii* and *Cebus capucinus* form mixed-species groups? *International Journal of Primatology, 10*, 103-114.

Boinski, S. (1999). The social organizations of squirrel monkeys: implications for ecological models of social evolution. *Evolutionary Anthropology: Issues, News, and Reviews, 8,* 101-112.

Boinski, S. (2002). *The monkeys of Suriname.* STINASU, Stichting Natuurbehound Suriname.

Boinski, S., & Scott, P. E. (1988). Association of birds with monkeys in Costa Rica. *Biotropica*, *20,* 136-143.

Boinski, S. & Garber, P. A. (2000). *On the move: how and why animals travel in groups*. University of Chicago Press.

Boinski, S., Quatrone, R. P., & Swartz, H. (2000). Substrate and Tool Use by Brown Capuchins in Suriname: Ecological Contexts and Cognitive Bases. *American Anthropologist, 102,* 741-761.

Boinski, S., Kauffman, L., Westoll, A., Stickler, C. M., Cropp, S., & Ehmke, E. (2003). Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii, S. boliviensis, and S. sciureus*). *Behaviour, 140,* 1421-1467.

Boinski, S., Kauffman, L., Ehmke, E., Schet, S., & Vreedzaam, A. (2005). Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii, S. boliviensis* and *S. sciureus*): I. Divergent costs and benefits. *Behaviour, 142*, 525-632.

Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). *Ucinet for Windows: Software for Social Network Analysis*. Analytic Technologies.

Boubli, J., Rylands, A. B., de la Torre, S., & Stevenson, P. (2008). *Saimiri sciureus*. The IUCN Red List of Threatened Species 2008: e.T41537A10494364. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41537A10494364.en. Downloaded on 28 July 2020.

Boubli, J., Alves, S. L., Buss, G., Carvalho, A., Ceballos-Mago, N., Lynch Alfaro, J., Messias, M., Mittermeier, R. A., Palacios, E., Ravetta, A., Rumiz, D. I., Rylands, A. B., Stevenson, P., & de la Torre, S. (2018a). *Sapajus apella*. The IUCN Red List of Threatened Species 2018: e.T39949A70611337. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T39949A70611337.en. Downloaded on 26 February 2020.

Boubli, J., Mittermeier, R. A., Urbani, B., & de Azevedo, R. (2018b). *Chiropotes sagulatus*. The IUCN Red List of Threatened Species 2018: e.T43891A17976546. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T43891A17976546.en. Downloaded on 28 July 2020.

Bowler, M. T., Buchanan-Smith, H. M., & Whiten, A. (2012). Assessing public engagement with science in a university primate research centre in a national zoo. *PloS ONE*, *7*, 1-9.

Box. H. O. (1991). Training for life after release: simian primates as examples. In J.H.W. Gipps (Ed.), *Beyond Captive Breeding: Reintroducing Endangered Mammals to the Wild* (pp. 111-123). Oxford University Press.

Boyd, R., & Silk, J. B. (1983). A method for assigning cardinal dominance ranks. *Animal Behaviour, 31*, 45-58.

BPS. (2012). Guidelines for psychologists working with animals. The British Psychological Society.

Bradbury, J. W., & Vehrencamp, S. L. (1977). Social organization and foraging in emballonurid bats. *Behavioral Ecology and Sociobiology, 2*, 1-17.

Brando, S., & Buchanan-Smith, H. M. (2018). The 24/7 approach to promoting optimal welfare for captive wild animals. *Behavioural Processes*, *156*, 83-95.

Braune, P., Schmidt, S., & Zimmermann, E. (2005). Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (*Microcebus ravelobensis*): the role of olfactory and acoustic signals. *Behavioral Ecology and Sociobiology, 58*, 587-596.

Brawer, M. (1991). Suriname. In *Atlas of South America* (pp. 120-123). The Macmillan Press Ltd.

Brent, L., Koban, T., & Evans, S. (2003). The influence of temperature on the behavior of captive mother-infant baboons. *Behaviour, 140*, 209-224.

Brown, M. (2013). Food and range defence in group-living primates. *Animal Behaviour*, *85*, 807-816.

Buchanan-Smith, H. M. (1990). Polyspecific association of two tamarin species, *Saguinus labiatus* and *Saguinus fuscicollis*, in Bolivia. *American Journal of Primatology*, *22*, 205-214.

Buchanan-Smith, H. M. (1997). Environmental control; an important feature of good captive callitrichid environments. In C. Pryce, L. Scott, & C. Schnell (Eds.), *Marmosets and Tamarins in Biological and Biomedical Research* (pp. 47-53). DSSD Imagery.

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. (1999a). Tamarin polyspecific associations: forest utilization and stability of mixed-species groups. *Primates, 40*, 233-247.

Buchanan-Smith, H. M. (1999b). Exploration of unfamiliar areas and detection of potentially threatening objects in single- and mixed-species groups of tamarins. *International Journal of Comparative Psychology, 12,* 2-20.

Buchanan-Smith, H. M. (2012). Mixed-species exhibition of Neotropical primates: analysis of species combination success. *International Zoo Yearbook*, *46*, 150-163.

Buchanan-Smith, H. M., Hardie, S. M., Caceres, C., & Prescott, M. J. (2000). Distribution and forest utilization of *Saguinus* and other primates of the Pando Department, northern Bolivia. *International Journal of Primatology, 21*, 353-379.

Buchanan-Smith, H. M., Prescott, M. J., & Cross, N. J. (2004). What factors should determine cage sizes for primates in the laboratory? *Animal Welfare, 13,* 197-201.

Buchanan-Smith, H. M., Griciute, J., Daoudi, S., Leonardi, R., & Whiten, A. (2013). Interspecific interactions and welfare implications in mixed species communities of capuchin (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) over 3 years. *Applied animal behaviour science*, *147*, 324-333.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press.

Busse, C. (1980). Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. *Botswana Notes and Records*, 15-21.

Buzzard, P. J. (2010). Polyspecific associations of *Cercopithecus campbelli* and *C. petaurista* with *C. diana*: what are the costs and benefits? *Primates*, *51*, 307-314.

Byrne, R. W. (1982). Primate vocalisations: structural and functional approaches to understanding. *Behaviour, 80,* 241-258.

Byrne, R. W., & Whiten, A. (1997). Machiavellian intelligence. In R.W. Byrne & A. Whiten (Eds.), *Machiavellian intelligence II: Extensions and evaluations* (pp. 1-23). Cambridge University Press.

Byrne, R. W., & Corp, N. (2004). Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*, 1693-1699.

Byrne, R. W., Noser, R., Bates, L. A., & Jupp, P. E. (2009). How did they get here from there? Detecting changes of direction in terrestrial ranging. *Animal Behaviour, 77,* 619-631.

Caine, N. G., & Marra, S. L. (1988). Vigilance and social organization in two species of primates. *Animal Behaviour*, *36*, 897-904.

Caldwell, G. S. (1981). Attraction to tropical mixed-species heron flocks: proximate mechanism and consequences. *Behavioral Ecology and Sociobiology*, *8*, 99-103.

Camazine, S., Deneubourg, J. L., Franks, N. R., Sneyd, J., Bonabeau, E., & Theraula, G. (2003). *Self-organization in biological systems*. Princeton University Press.

Campbell, E. Q. (1958). Some social psychological correlates of direction in attitude change. *Social Forces, 36*, 335-340.

Canale, G. R., Guidorizzi, C. E., Kierulff, M. C. M., & Gatto, C. A. F. R. (2009). First record of tool use by wild populations of the yellow-breasted capuchin monkey (*Cebus xanthosternos*) and new records for the bearded capuchin (*Cebus libidinosus*). *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *71*, 366-372.

Caraco, T. (1979). Time budgeting and group size: a theory. *Ecology*, *60*, 611-617.

Caraco, T. (1981). Risk-sensitivity and foraging groups. *Ecology, 62*, 527-531.

Caraco, T., & Wolf, L. L. (1975). Ecological determinants of group sizes of foraging lions. *The American Naturalist*, *109*, 343-352.

Carlstead, K. (1996). Effects of captivity on the behavior of wild mammals. In D.G. Kleiman, M.E. Allen, K.V. Thompson, S. Lumpkin, (Eds.), *Wild Mammals in Captivity* (pp. 317-333). University of Chicago Press.

Chance, M. R. (1967). Attention structure as the basis of primate rank orders. *MAN*, *2*, 503-518.

Chamove, A. S. & Anderson, J. R. (1989). Examining environmental enrichment. In: E.F. Segal (Ed.) *Housing, Care and Psychological Well-being of Captive and Laboratory Primates* (pp. 183-202). Noyes Publications.

Chapman, C. A. (1989). Primate seed dispersal: the fate of dispersed seeds. *Biotropica, 21*, 148-154.

Chapman, C. A. (1986). *Boa constrictor* predation and group response in white-faced *Cebus* monkeys. *Biotropica, 18,* 171-172.

Chapman, C. A. (1990). Ecological constraints on group size in 3 species of neotropical primates. *Folia Primatologica, 55*, 1-9.

Chapman, C. A. (1995). Primate seed dispersal: coevolution and conservation implications. *Evolutionary Anthropology: Issues, News, and Reviews, 4*, 74-82.

Chapman, C. A., & Lefebvre, L. (1990). Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behaviour*, *39*, 891-896.

Chapman, C. A. & Chapman, L. J. (2000a). Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. *International Journal of Primatology, 21*, 565-585.

Chapman, C. A. & Chapman, L. J. (2000b). Interdemic variation in mixed-species association patterns: common diurnal primates of Kibale National Park, Uganda. *Behavioural Ecology and Socieobiology, 47,* 129-139.

Chapman, C. A., & Russo, S. E. (2011). Primate seed dispersal. In C. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder, & R.M. Stumpf (Eds.), *Primates in perspective* (pp. 510-525). Oxford University Press.

Charles-Dominique, P. (1977). *Ecology and behaviour of nocturnal primates.* Columbia University Press.

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception–behavior link and social interaction. *Journal of Personality and Social Behaviour, 76,* 893–910.

Chepko-Sade, B. D., & Sade, D. S. (1979). Patterns of group splitting within matrilineal kinship groups: A study of social group structure in Macaca mulatta (Cercopithecidae: Primates). *Behavioral Ecology and Sociobiology, 5*, 67-86.

Cheney, D. L. (1978a). Interactions of immature male and female baboons with adult females. *Animal Behaviour*, *26*, 389-408.

Cheney, D. L. (1978b). The play partners of immature baboons. *Animal Behaviour*, *26*, 1038-1050.

Childress, M. J., & Lung, M. A. (2003). Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal behaviour*, *66*, 389-398.

Claidière, N., Messer, E. J., Hoppitt, W., & Whiten, A. (2013). Diffusion dynamics of socially learned foraging techniques in squirrel monkeys. *Current Biology, 23*, 1251-1255.

Clark, C. W. (1995). Application of US Navy underwater hydrophone arrays for scientific research on whales. *Reports International Whaling Commission*, *45*, 210-212.

Clark, C. W., & Mangel, M. (1984). Foraging and flocking strategies: information in an uncertain environment. *The American Naturalist*, *123*, 626-641.

Clark, F. E., & Melfi, V. A. (2011). Environmental enrichment for a mixed-species nocturnal mammal exhibit. *Zoo Biology, 331*, 397-413.

Clarke, S., Juno, C., & Maple, T.L. (1982). Behavioural effects of a change in the physical environment: A pilot study of captive chimpanzees. *Zoo Biology, 1,* 371-380.

Clay, Z., & Zuberbühler, K. (2009). Food-associated calling sequences in bonobos. *Animal Behaviour*, *77*, 1387-1396.

Clutton-Brock, T. H. (1974). Primate social organisation and ecology. *Nature*, *250*, 539-542.

Clutton-Brock, T. H. (1975). Feeding behaviour of red colobus and black and white colobus in east Africa. *Folia Primatologica, 23*, 165–207.

Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature, 462*, 51-57.

Cody, M. L. (1971). Finch flocks in the Mohave Desert. *Theoretical Population Biology, 2*, 142-158.

Coelho, C. G., Falotico, T., Izar, P., Mannu, M., Resende, B. D., Siqueira, J. O., & Ottoni, E. B. (2015). Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.). *Animal cognition*, *18*, 911-919.

Coleing, A. (2009). The application of social network theory to animal behaviour. *Bioscience Horizons, 2*, 32-43.

Coleman, K. (2012). Individual differences in temperament and behavioral management practices for nonhuman primates. *Applied animal behaviour science, 137*, 106-113.

Connor, R. C. (2007). Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 587-602.

Conradt, L. (1998). Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*, 1359-1368.

Conradt, L., & List, C. (2008). Group decisions in humans and animals: a survey. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*, 719-742.

Conradt, L., & Roper, T. J. (2000). Activity synchrony and social cohesion: a fission-fusion model. *Proceedings of the Royal Society B*, *267*, 2213–2218.

Conradt, L. & Roper, T. J. (2003). Group decision-making in animals. *Nature*, *421*, 155–158.

Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology & Evolution*, *20*, 449-456.

Cooper, M. A., Bernstein, I. S., Fragaszy, D. M. & de Waal, F. B. M. (2001). Integration of new males into four social groups of tufted capuchins (*Cebus apella*). *International Journal of Primatology, 22*, 663-683.

Cords, M. (1987). Mixed-species association of Cercopithecus monkeys in the Kakamega Forest, Kenya. *University of California Publications Zoology, 117*, 1–109.

Cords, M. (1990a). Mixed-species association of east African guenons: general patterns or specific examples. *American Journal of Primatology, 21,* 101-114.

Cords, M. (1990b). Vigilance and mixed-species association of some East African forest monkeys. *Behavioral Ecology and Sociobiology, 26*, 297-300.

Cords, M. (1997). Friendships, alliances, reciprocity and repair. In In R.W. Byrne & A. Whiten (Eds.), *Machiavellian intelligence II: Extensions and evaluations* (pp. 24-49). Cambridge University Press.

Cords, M., & Aureli, F. (1993). Patterns of reconciliation among juvenile long-tailed macaques. In M.E. Pereira & L.A. Fairbanks (Eds.) *Juvenile primates: Life history, development and behavior* (pp. 271-284). The University of Chicago Press.

Cortes-Ortíz, L., Urbani, B., Boubli, J., de Melo, F.R., Mittermeier, R.A., & dos Santos, M. (2020). *Alouatta macconnelli*. The IUCN Red List of Threatened Species 2020: e.T40642A17926817. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T40642A17926817.en. Downloaded on 28 July 2020.

Cortopassi, K. A., & Bradbury, J. W. (2006). Contact call diversity in wild orange-fronted parakeet pairs, *Aratinga canicularis. Animal Behaviour, 71*, 1141-1154.

Coss, R. G., & Owings, D. H. (1977). Snake mobbing by California ground squirrels: adaptive variation and ontogeny. *Behaviour*, *62*, 50-68.

Costello, R. K., Dickinson, C., Rosenberger, A. L., Boinski, S., & Szalay, F. S. (1993). Squirrel monkey (genus *Saimiri*) taxonomy. In (Eds.) FS, Szalay, S, Boinski, AL, Rosenberger, C, Dickinson & RK, Costello. *Species, species concepts and primate evolution* (pp. 177-210). Springer, Boston, MA.

Couzin, I. D. (2006). Behavioral ecology: social organization in fission–fusion societies. *Current Biology*, *16*, R169-R171.

Couzin, I. D. (2009). Collective cognition in animal groups. *Trends in cognitive sciences, 13,* 36-43.

Couzin, I. D., & Krause, J. (2003). Self-organization and collective behavior in vertebrates. *Advances in the Study of Behaviour, 74,* 1735-1742.

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*, 513-516.

Coye, C., Ouattara, K., Zuberbühler, K., & Lemasson, A. (2015). Suffixation influences receivers' behaviour in non-human primates. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20150265.

Crofoot, M. C., Rubenstein, D. I., Maiya, A. S., & Berger-Wolf, T. Y. (2011). Aggression, grooming and group-level cooperation in white-faced capuchins (Cebus capucinus): insights from social networks. *American Journal of Primatology*, *73*, 821-833.

Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton University Press.

Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D., & Krause, J. (2005). Assortative interactions and social networks in fish. *Oecologia, 143*, 211-219.

Croft, D. P., Madden, J. R., Franks, D. W., & James, R. (2011). Hypothesis testing in animal social networks. *Trends in ecology & evolution*, *26*, 502-507.

Curio, E. (1976). *The ethology of predation.* Springer-Verlag.

Custance, D. M., Whiten, A., & Fredman, T. (2002). Social learning and primate reintroduction. *International Journal of Primatology, 23,* 479-499.

Dalton, R., & Buchanan-Smith, H.M. (2005). A mixed species exhibit for Goeldi's monkeys and pygmy marmosets at Edinburgh zoo. *International Zoo Yearbook, 39,* 176-184.

Daoudi, S., Badihi, G., & Buchanan-Smith, H. M. (2017). Is mixed-species living cognitively enriching? Enclosure use and welfare in two captive groups of tufted capuchins (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*). *Animal Behavior and Cognition, 4*, 51-69.

Darwin, C. (1964). *On the origin of species: A facsimile of the first edition*. Harvard University Press.

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology* (4th ed.). John Wiley & Sons.

Dawkins, M. S. (1998). Evolution and animal welfare. *Quarterly Review of Biology, 73*, 305–328.

de Almeida Rocha, J. M., De Vleeschouwer, K. M., Reis, P. P., Grelle, C. E. D. V., & Oliveira, L. C. (2015). Do habitat use and interspecific association reflect predation risk for the golden-headed lion tamarin (*Leontopithecus chrysomelas*)? *International Journal of Primatology, 36*, 1198-1215.

de Ruiter, J. R. (1986). The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (*Cebus olivaceus*). *Behaviour*, *98*, 240– 258.

de Waal, F. B. M. (1982). *Chimpanzee politics*. Jonathan Cape.

de Waal, F. B. (1986). The integration of dominance and social bonding in primates. *The Quarterly review of biology, 61,* 459-479.

de Waal, F. B. D., & Ren, R. (1988). Comparison of the reconciliation behavior of stumptail and rhesus macaques. *Ethology*, *78*, 129-142.

de Waal, F. B., & Yoshihara, D. (1983). Reconciliation and redirected affection in rhesus monkeys. *Behaviour, 85*, 224-241.

Delm, M. M. (1990). Vigilance for predators: detection and dilution effects. *Behavioral Ecology and Sociobiology*, *26*, 337-342.

Demment, M. W. (1983). Feeding ecology and the evolution of body size of baboons. *African Journal of Ecology, 21*, 219-233.

Demment, M. W., & van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, *125*, 641-672.

Dempster, J. P. (1975). *Animal Population Ecology*. London: Academic Press.

Dostálková, I., & Špinka, M. (2007). Synchronization of behaviour in pairs: The role of communication and consequences in timing. *Animal Behavior*, *74,* 1735–1742.

Dickens, M. (1955). A statistical formula to quantify the “spread-of-participation” in group discussion. *Speech Monographs, 22*, 28-31.

Dietz, J. M., Baker, A. J., & Miglioretti, D. (1994). Seasonal variation in reproduction, juvenile growth, and adult body mass in golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology, 34*, 115-132.

Drews, C. (1993). The concept and definition of dominance in animal behaviour. *Behaviour, 125*, 283-313.

Dufour, V., Sueur, C., Whiten, A., & Buchanan-Smith, H. M. (2011). The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *American journal of primatology*, *73*, 802-811.

Dugatkin, L. A. (1997). *Cooperation among animals: an evolutionary perspective*. Oxford University Press.

DuMond, F. V. (1968). The squirrel monkey in a seminatural environment. In L.A. Rosenblum & R.W. Cooper (Eds.), *The squirrel monkey*. Academic Press.

DuMond, F. V. & Hutchinson, T. C. (1967). Squirrel monkey reproduction: the “fatted” male phenomenon and seasonal spermatogenesis. *Science, 158,* 1067-1070.

Dunbar, R. I. M. (1988). *Primate Social Systems*. Croom Helm.

Dunbar, R. I. M. (1989). Social systems as optimal strategy sets: the costs and benefits of sociality. In V. Standen & R.A. Foley (Eds.) *Comparative socioecology*: *the behavioural ecology of humans and other mammals* (pp. 73-88). Blackwells Scientific Publications.

Dunbar, R. I. M., & Dunbar, P. (1988). Maternal time budgets of gelada baboons. *Animal Behaviour, 36*, 970-980.

Dunbar, R. I. M., & Shi, J. (2008). Sex differences in feeding activity results in sexual segregation of feral goats. *Ethology, 114*, 444-451.

Dunbar, R. I., & Spoors, M. (1995). Social networks, support cliques, and kinship. *Human Nature*, *6*, 273-290.

Duplaix, N. (1980). Observations on the ecology and behavior of the giant river otter, *Pteronura brasiliensis*, in Suriname. *Review d’Écolologie (Terre Vie), 34,* 495-620.

Duranton, C., & Gaunet, F. (2015). *Canis sensitivus*: Affiliation and dogs’ sensitivity to others’ behavior as the basis for synchronization with humans? *Journal of Veterinary Behavior, 10*, 513–524.

Duranton, C., & Gaunet, F. (2016). Behavioural synchronization from an ethological perspective: overview of its adaptive value. *Adaptive Behavior, 24,* 181-191.

Dyer, J. R., Johansson, A., Helbing, D., Couzin, I. D., & Krause, J. (2008). Leadership, consensus decision making and collective behaviour in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 781-789.

Eaton, S. W. (1953). Wood warblers wintering in Cuba. *The Wilson Bulletin, 65*, 169-174.

Ebensperger, L. A., Hurtado, M. J., & Ramos-Jiliberto, R. (2006). Vigilance and collective detection of predators in degus (*Octodon degus*). *Ethology, 112,* 879-887.

Eckardt, W., & Zuberbühler, K. (2004). Cooperation and competition in two forest monkeys. *Behavioral Ecology*, *15*, 400-411.

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews*, *64*, 13-33.

Emlen, S. T. (1982). The evolution of helping. I. An ecological constraints model. *The American Naturalist*, *119*, 29-39.

Emlen, S. T. (1984). Cooperative breeding in birds and mammals. In J. R. Krebs & N. B. Davies (eds.) *Behavioural Ecology* (pp. 305–339). Oxford: Blackwell Scientific.

Emlen, S. T. (1994). Benefits, constraints and the evolution of the family. *Trends in Ecology and Evolution, 9*, 282–285.

Engel, J., & Lamprecht, J. (1997). Doing what everybody does? A procedure for investigating behavioural synchronization. *Journal of Theoretical Biology, 185*, 255-262.

Estevez, J., & Christman, M.C. (2006). Analysis of the movement and use of space of animals in confinement: The effect of sampling effort. *Applied Animal Behaviour Science, 97,* 221-240.

Fairbanks, L. A., & McGuire, M. T. (1984). Determinants of fecundity and reproductive success in captive vervet monkeys. *American Journal of Primatology, 7*, 27-38.

FAO. (2015). Global forest resources assessment, desk reference. Retrieved from http://www.fao.org/3/a-i4808e.pdf

Farm Animal Welfare Council (FAWC). (1979, 5 December). Farm Animal Welfare Council Press Statement.

Farm Animal Welfare Council (FAWC). (1992). FAWC updates the five freedoms. *Veterinary Record, 17,* 357.

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods in Ecology and Evolution, 4,* 1187-1194.

Farine, D. R., Aplin, L. M., Garroway, C. J., Mann, R. P., & Sheldon, B. C. (2014). Collective decision making and social interaction rules in mixed-species flocks of songbirds. *Animal behaviour, 95,* 173-182.

Farine, D. R., Aplin, L. M., Sheldon, B. C., & Hoppitt, W. (2015). Interspecific social networks promote information transmission in wild songbirds. *Proceedings of the Royal Society B: Biological Sciences, 282,* 20142804.

Farine, D. R., Garroway, C. J., & Sheldon, B. C. (2012). Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. *Animal Behaviour, 84*, 1271-1277.

Farine, D. R., & Milburn, P. J. (2013). Social organisation of thornbill-dominated mixed-species flocks using social network analysis. *Behavioral Ecology and Sociobiology, 67*, 321-330.

Fedigan, L. (1993). Sex differences and intersexual relations in adult white-faced capuchins (Cebus capucinus). *International Journal of Primatology, 14*, 853-877.

Fedigan, L. M., Carnegie, S. D., & Jack, K. M. (2008). Predictors of reproductive success in female white-faced capuchins (Cebus capucinus). *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists, 137*, 82-90.

Fernandez, E. J., Tamborski, M. A., Pickens, S. R., & Timberlake, W. (2009). Animal–visitor interactions in the modern zoo: Conflicts and interventions. *Applied Animal Behaviour Science, 120*, 1-8.

Fernandez, G. J., Capurro, A. F., & Reboreda, J. C. (2003). Effect of group size on individual and collective vigilance in Greater Rheas. Ethology, 109, 413–425.

Ferrari, S. F., & Lopes Ferrari, M. A. (1990). Predator avoidance behaviour in the buffy-headed marmoset, *Callithrix flaviceps. Primates, 31,* 323-338.

Ferreira, R. G., Izar, P., & Lee, P. C. (2006). Exchange, affiliation, and protective interventions in semifree-ranging brown capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, *68*, 765-776.

Field, A. (2009). *Discovering statistics using SPSS:(and sex and drugs and rock'n'roll)*. Sage

Ficthel, C. (2004). Reciprocal recognition of sifaka (*Propithecus verreauxi verreauxi*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. *Animal cognition*, *7*, 45-52.

Fichtel, C., Pyritz, L., & Kappeler, P. M. (2011). Coordination of group movements in non-human primates. In M. Boos, M. Kolbe, P.M. Kappeler, & T. Ellwart (Eds.), *Coordination in human and primate groups* (pp. 37-56). Springer, Berlin, Heidelberg.

Fichtel, C., Zucchini, W., & Hilgartner, R. (2011). Out of sight but not out of mind? Behavioral coordination in red-tailed sportive lemurs (*Lepilemur ruficaudatus*). *International journal of primatology*, 32, 1383-1396.

Finn, K. R., Silk, M. J., Porter, M. A., & Pinter-Wollman, N. (2019). The use of multilayer network analysis in animal behaviour. *Animal behaviour*, *149*, 7-22.

Fitzgibbon, C. D. (1990). Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Animal Behaviour, 39*, 1116-1126.

Fitzgibbon, C. D. (1994). The costs and benefits of predator inspection behaviour in Thomson's gazelles. *Behavioral Ecology and Sociobiology*, *34*, 139-148.

Flack, J. C., Girvan, M., De Waal, F. B., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature, 439,* 426-429.

Fleagle, J. G., & Mittermeier, R. A. (1980). Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *American Journal of Physical Anthropology, 52*, 301-314.

Fleagle, J. G., Mittermeier, R. A., & Skopec, A. L. (1981). Differential habitat use by *Cebus apella* and *Saimiri sciureus* in central Surinam. *Primates*, *22*, 361-367.

Fleagle, J. G. (1999). *Primate adaptation and evolution*. Academic Press.

Foerder, P., Chodorow, M., & Moore, D. E. (2013). Behavioural synchrony in two species of communally housed captive penguins. *Behaviour*, *150*, 1357-1374.

Ford, S. M., & Davis, L. C. (1992). Systematics and body size: implications for feeding adaptations in New World monkeys. *American Journal of Physical Anthropology, 88*, 415-468.

Foster, W. A., & Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature, 293*, 466-467.

Fragaszy, D. (1986). Time budgets and foraging behavior in wedge-capped capuchins (*Cebus olivaceus*): age and sex differences. In D. Taub, & F. King (Eds.). *Current perspectives in primate social dynamics* (pp. 159-174). Van Nostrand.

Fragaszy, D. (1990). Sex and age differences in the organisation of behaviour in wedge-capped capuchins, Cebus olivaceus. *Behavioral Ecology*, *1,* 81– 94.

Fragaszy, D. M., Visalberghi, E. & Fedigan, L. M. (2004). *The complete capuchin: the biology of the genus Cebus*. Cambridge University Press.

Fraser, O. N., Schino, G., & Aureli, F. (2008). Components of relationship quality in chimpanzees. *Ethology*, *114*, 834-843.

Frechette, J. L., Sieving, K. E., & Boinski, S. (2014). Social and personal information use by squirrel monkeys in assessing predation risk. *American Journal of Primatology, 76*, 956-966.

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 1785-1801.

Freese, C. H., & Oppenheimer, J. R. (1981). The capuchin monkeys, *Cebus apella*. In A.F. Coimbra-Filho, & R.A. Mittermeier (Eds.), *Ecology and Behavior of Neotropical Primates* (pp. 331-390). Academia Brasileira de Ciencias.

Galdikas, B. M., Teleki, G., Coelho Jr, A. M., Eckhardt, R. B., Fleagle, J. G., Hladik, C. M., Kelso, A. J., McGrew, W. C. Nash, L. T., Nishida, T., Paterson, J. D., Savage-Rumbaugh, S., Smith, E. O., Sugiyama, Y., & Wrangham, R. W. (1981). Variations in subsistence activities of female and male pongids: new perspectives on the origins of hominid labor division [and comments]. *Current Anthropology, 22*, 241-256.

Garber, P. A., & Lambert, J. E. (1998). Primates as seed dispersers: ecological processes and directions for future research. *American Journal of Primatology, 45*, 3-8.

Gartlan, J. S., & Struhsaker, T. T. (1972). Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa. *Journal of Zoology*, *168*, 221-265.

Gautier, J. P., & Gautier-Hion, A. (1969). Les associations polyspécifiques chez les Cercopithecidae du Gabon. *La Terre et la Vie, 116*, 164-201.

Gautier-Hion, A., & Gautier, J. P. (1974). Les associations polyspécifiques de Cercopithèques du Plateau de M'passa (Gabon) (Part 1 of 4). *Folia primatologica, 22*, 134-144.

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). Academic Press.

Gautier-Hion, A. (1980). Seasonal variations of diet related to species and sex in a community of Cercopithecus monkeys. *The Journal of Animal Ecology*, *49*, 237-269.

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., & 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.

Gautrais, J., Michelena, P., Sibbald, A., Bon, R., & Deneubourg, J. L. (2007). Allelomimetic synchronization in merino sheep. *Animal Behaviour*, *74,* 1443–1454.

Geist, V. (1974). On the relationship of social evolution and ecology in ungulates. *American zoologist, 14*, 205-220.

Ghiglieri, M. P. (1984). Feeding ecology and sociality of chimpanzees in the Kibale Forest, Uganda. In Rodman, P. S., and Cant, J. G. H. (Eds.). *Adaptations for Foraging in Non-Human Primates* (pp. 161-194). Columbia University Press.

Ginsberg, J. R., & Young, T. P. (1992). Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, *44*, 377-379.

Giraldeau, L. A., & Beauchamp, G. (1999). Food exploitation: searching for the optimal joining policy. *Trends in Ecology & Evolution*, *14*, 102-106.

Gochfeld, M., & Burger, J. (1994). Vigilance in African mammals: differences among mothers, other females, and males. *Behaviour, 131*, 153-169.

Gold, K. C. (1997). The conservation role of primate exhibits in the zoo. *Primate conservation: the role of zoological parks*, 43-61.

Goodale, E., Ratnayake, C. P., & Kotagama, S. W. (2014). Vocal mimicry of alarm-associated sounds by a drongo elicits flee and mobbing responses from other species that participate in mixed-species bird flocks. *Ethology*, *120*, 266-274.

Goodale, E., Beauchamp, G. & Ruxton, G. D. (2017). *Mixed-species groups of animals*. Academic Press.

Goodenough, A. E., McDonald, K., Moody, K., & Wheeler, C. (2019). Are "visitor effects" overestimated? Behaviour in captive lemurs is mainly driven by co-variation with time and weather. *Journal of Zoo and Aquarium Research*, *7*, 59-66.

Gosselin-Ildari, A. D., & Koenig, A. (2012). The effects of group size and reproductive status on vigilance in captive *Callithrix jacchus*. *American Journal of Primatology*, *74*, 613– 621.

Gould, L. (1997). Intermale affiliative behavior in ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. *Primates, 38*, 15-30.

Grove, M. (2012). Space, time, and group size: a model of constraints on primate social foraging. *Animal Behaviour*, *83*, 411-419.

Groves, C. P. (2001). *Primate taxonomy.* Washington: Smithsonian Institution Press.

Hall, J., Inogwabini, B. I., Williamson, E., Omari, I., Sikubwabo, C., & White, L. (1997). A survey of elephants (*Loxodonta africana*) in the Kahuzi-Biega National Park lowland sector and adjacent forest in eastern Zaire. *African Journal of Ecology*, *35*(3), 213-223.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, *7*, 17-52.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*, 295-311.

Hammond, D. S. (2005). *Tropical forests of the Guiana Shield: ancient forests in a modern world*. CABI Publishing.

Hanneman, R.A. & Riddle, M. (2005). *Introduction to Social Network Methods*. University of California, Riverside. Published in digital form at: http://faculty.ucr.edu/~hanneman/.

Hanson, M. T., & Coss, R. G. (2001). Age differences in arousal and vigilance in California ground squirrels (*Spermophilus beecheyi*). *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology*, *39*, 199-206.

Hardie, S. M., & Buchanan-Smith, H. M. (1997). Vigilance in single-and mixed-species groups of tamarins (*Saguinus labiatus* and *Saguinus fuscicollis*). *International Journal of Primatology, 18,* 217-234.

Harrison, M. J. (1983). Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. *Animal Behaviour, 31*, 969-977.

Harvey, I. F. (1994). Strategies of behaviour. In T.R. Halliday & P.J.B. Slater (Eds.), *Behaviour and evolution* (pp. 106-149). Cambridge University Press.

Haude, R. H., Graber, J. G., & Farres, A. G. (1976). Visual observing by rhesus monkeys: some relationships with social dominance rank. *Animal learning & behavior*, *4*, 163-166.

Hauser, M. D. (1992). Costs of deception: cheaters are punished in rhesus monkeys (*Macaca mulatta*). *Proceedings of the National Academy of Sciences*, *89*, 12137-12139.

Hebert, P. L., & Bard, K. (2000). Orangutan use of vertical space in an innovative habitat. Zoo Biology: Published in affiliation with the *American Zoo and Aquarium Association, 19*, 239-251.

Hediger, H. (1950). *Wild animals in captivity.* Butterworth.

Heise, C. D., & Moore, F. R. (2003). Age-related differences in foraging efficiency, molt, and fat deposition of Gray Catbirds prior to autumn migration. *The Condor, 105*, 496-504.

Hemelrijk, C. K. (1990a). Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behaviour*, *39*, 1013-1029.

Hemelrijk, C. K. (1990b). A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. *Journal of theoretical Biology, 143*, 405-420.

Hemelrijk, C. K. (1994). Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, *48*, 479-481.

Hemelrijk, C. K. (2000). Towards the integration of social dominance and spatial structure. *Animal Behaviour, 59,* 1035-1048.

Henzi, S. P., Byrne, R. W., & Whiten, A. (1992). Patterns of movement by baboons in the Drakensberg mountains: primary responses to the environment. *International Journal of Primatology, 13*, 601-629.

Hershkowitz, P. (1977). *Living new world monkeys (Platyrrhini) with an introduction to primates. Vol 1.* Chicago University Press.

Hershkowitz, P. (1984). Taxonomy of squirrel monkeys genus *Saimiri* (Cebidae, Platyrrhini): a preliminary report with description of a hitherto unnamed form. *American Journal of Primatology, 7*, 155-210.

Herzing, D. L., & Johnson, C. M. (1997). Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985–1995. *Aquatic Mammals, 23*, 85–99. Field observation

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 Rio Blanco, Peruvian Amazonia. *American Journal of Primatology, 21,* 115-127.

Heymann, E. (1990b). Reactions of wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis* to avian predators. *International Journal of Primatology, 11,* 327–337

Heymann, E. W. (1997). The relationship between body size and mixed-species troops of tamarins (*Saguinus* spp.). *Folia Primatologica, 68*, 287-295.

Heymann, E. W. & Buchanan-Smith, H. M. (2000). The behavioural ecology of mixed-species troops of callitrichine primates. *Biological Reviews*, *75*, 169–190.

Heymann, E. W., Sicchar Valdez, L. A., & Tapia, R. J. (1996). Experiences with mixed-species housing of tamarins, *Saguinus fuscicollis* and *Saguinus mystax* (Primates: Callitrichidae), in an outdoor enclosure. *Zoologische Garden (NF), 66*, 381–390.

Hill, W. C. O. (1960). *Primates, Comparative Anatomy and Taxonomy: Vol. 4, Cebidae Part A*. Edinburgh University Press.

Hill, W. C. O. (1962). *Primates, Comparative Anatomy and Taxonomy: Vol. 5, Cebidae Part B*. Edinburgh University Press.

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*, 245, 447-456.

Hinde, R. A. (1966). *Animal behaviour: a synthesis of ethology and comparative psychology.* McGraw-Hill.

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man, 11,* 1-17.

Hinde, R. A. (1983a). A conceptual framework. In: R.A., Hinde (Ed.), *Primate Social Relationships* (pp. 1-7). Blackwell Scientific Publications.

Hinde, R. A. (1983b). Ultimate factors determining individual strategies, relationships and social structure. In, R.A. Hinde (Ed.), *Primate social relationships: an integrated approach* (pp. 250-255). Blackwell Scientific Publications.

Hiraiwa-Hasegawa, M. (1997). Development of sex differences in nonhuman primates. In M.E. Morbeck, A. Galloway, & A.L. Zihlman (Eds.). *The Evolving Female: A Life History Perspective* (pp.69-75). Princeton University Press.

Hirsch, B. T. (2002). Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, *52*, 458-464.

Hirsch, B. T. (2007). Spoiled brats: an extreme form of juvenile dominance in the ring-tailed coati (*Nasua nasua*). *Ethology, 113*, 446–456.

Hirsch, B. T., Stanton, M. A., & Maldonado, J. E. (2012). Kinship shapes affiliative social networks but not aggression in ring-tailed coatis. *PloS one*, *7*, e37301.

Hladik, A., & Hladik, C. M. (1969). Rapports trophiques entre vegetation et primates dans la forêt de Barro Colorado (Panama). *Terre Vie, 23*, 25-117.

Hladik, C. M., Hladik, A., Bousset, J., Valdebouze, P., Viroben, G., & Delort-Laval, J. (1971). Le régime alimentaire des Primates de l'île de Barro-Colorado (Panama). *Folia primatologica*, *16*, 85-122.

Hladik, C.M. (1975). Ecology, diet, and social patterning in Old and New World primates. In R.H, Tuttle (Ed.), *Socioecology and psychology of primates* (pp. 3-35). Mouton Publishers.

Holekamp, K. E., Sakai, S. T., & Lundrigan, B. L. (2007). Social intelligence in the spotted hyena (*Crocuta crocuta*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 523-538.

Holenweg, A. K., Noë, R., & Schabel, M. (1996). Waser's gas model applied to associations between red colobus and Diana monkeys in the Tai National Park, Ivory Coast. *Folia Primatologica*, *67*, 125-136.

Hosey, G. (2005). How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science, 90,* 107–129.

Howell, C. P., & Cheyne, S. M. (2019). Complexities of using wild versus captive activity budget comparisons for assessing captive primate welfare. *Journal of Applied Animal Welfare Science, 22*, 78-96.

Huber, O. (2005). Diversity and vegetation types in the Guayana Region, an overview. *Biologiske Skrifter, 55*, 169–188.

Humphrey, N. K. (1976). The social function of intellect. In P.P.G. Bateson & R.A. Hinde (Eds.). *Growing points in ethology* (pp. 303-317). Cambridge University Press.

Huntingford, F. (1984). *The Study of Animal Behaviour*. Chapman & Hall.

Hutchins, M., & Conway, W. G. (1995). Beyond Noah's Ark: the evolving role of modern zoological parks and aquariums in field conservation. *International Zoo Yearbook, 34*,117–130.

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, *2*, 143-155.

Isbell, L. A. (1994). Predation on primates: ecological patterns and evolutionary consequences. *Evolutionary Anthropology: Issues, News and Reviews,3,* 61-71.

Itoh, N., & Nishida, T. (2007). Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. *Primates*, *48*, 87-96.

IUCN (2020, July 28). The IUCN Red List of Threatened Species. Version 2020-2. Retrieved from: https://www.iucnredlist.org

IUDZG, C. (1993). The world zoo conservation strategy. *The Role of the Zoos and Aquaria of the World in Global Conservation. International Union of the Directors of Zoological Gardens and the Conservation Breeding Specialist Group, IUCN/SSC.*

Iwamoto, T. (1987). Food and energetics of provisioned wild Japanese macaques (*Macaca fuscata*). In: J.E. Fa & C.H. Southwick (Eds.). *Ecology and behavior of food-enhanced primate groups* (pp 79–94). Alan R. Liss, Inc.

Iwamoto, T., & Dunbar, R. I. M. (1983). Thermoregulation, habitat quality and the behavioural ecology of gelada baboons. *The Journal of Animal Ecology*, *52*, 357-366.

Iwamoto, T., Mori, A., Kawai, M., & Bekele, A. (1996). Anti-predator behavior of gelada baboons. *Primates*, *37*, 389-397.

Izawa, K. (1975). Foods and feeding behavior of monkeys in the upper Amazon basin. *Primates, 16*, 295-316.

Izawa, K. (1976). Group sizes and compositions of monkeys in the upper Amazon basin. *Primates, 17*, 367-399.

Izawa, K. (1980). Social behavior of the wild black-capped Capuchin (*Cebus apella*). *Primates*, *21*, 443-467.

Jack, K. M. (2011). The Cebines: toward an explanation of variable social structure. In C. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder, & R.M. Stumpf (Eds.), *Primates in perspective* (pp. 108-121). Oxford University Press.

Jack, K., & Fedigan, L. M. (2004a). The demographic and reproductive context of male replacements in *Cebus capucinus*. *Behaviour, 141*, 755-775.

Jack, K. M., & Fedigan, L. (2004b). Male dispersal patterns in white-faced capuchins, *Cebus capucinus*: Part 2: patterns and causes of secondary dispersal. *Animal behaviour, 67*, 771-782.

James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). *An introduction to statistical learning* (Vol. 112, pp. 3-7). Springer.

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. (1990). Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour, 40*, 922-934.

Janson, C. H., & Boinski, S. (1992). Morphological and behavioral adaptations for foraging in generalist primates: the case of the cebines. *American Journal of Physical Anthropology*, *88*, 483-498.

Janson, C. H., & Goldsmith, M. L. (1995). Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology*, *6*, 326-336.

Jendry, C. (1997). Partners in conservation: establishing *in situ* partnerships to aid mountain gorillas and people in range countries. *Primate conservation: the role of zoological parks*, 199-213.

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science, 153*, 501-506.

Jones, C. B. (1980). The functions of status in the mantled howler monkey, *Alouatta palliata Gray*: intraspecific competition for group membership in a folivorous Neotropical primate. *Primates*, 21, 389-405.

Kamilar, J., & Pokempner, A. (2008). Does body mass dimorphism increase male–female dietary niche separation? A comparative study of primates. *Behaviour, 145*, 1211-1234.

Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J., & Call, J. (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American journal of primatology*, *73*, 758-767.

Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, *50*, 343-356.

Kawamura, S. (1958). The matriarchal social order in the Minoo-B troop - A study on the rank system of Japanese macaques. *Primates, 1,* 149–156.

Kay, R. F., Plavcan, J. M., Glander, K. E., & Wright, P. C. (1988). Sexual selection and canine dimorphism in New World monkeys. *American Journal of Physical Anthropology, 77*, 385-397.

Kazahari, N., & Agetsuma, N. (2008). Social factors enhancing foraging success of a wild group of Japanese macaques (*Macaca fuscata*) in a patchy food environment. *Behaviour, 6,* 843-860.

Keddy, P. A. (1989). *Competition.* Chapman & Hall.

Kenagy, G. J., & Trombulak, S. C. (1986). Size and function of mammalian testes in relation to body size. *Journal of Mammalogy, 67*, 1-22.

Kenward, R. E. (1978). Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *The Journal of Animal Ecology*, *47*, 449-460.

Kerl, J., & Rothe, H. (1996). Influence of cage size and cage equipment on physiology and behavior of common marmosets (*Callithrix jacchus*). *Laboratory Primate Newsletter, 35,* 10–13.

Kerridge, F. J. (2005). Environmental enrichment to address behavioral differences between wild and captive black-and-white ruffed lemurs (*Varecia variegata*). *American Journal of Primatology: Official Journal of the American Society of Primatologists, 66*, 71-84.

Keulartz, J. (2015). Captivity for conservation? Zoos at a crossroads. *Journal of Agricultural and Environmental Ethics, 28*, 335-351.

Key, C., & Ross, C. (1999). Sex differences in energy expenditure in non–human primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*, 2479-2485.

Kimura, R. (1998). Mutual grooming and preferred associate relationships in a band of free-ranging horses. *Applied Animal Behaviour Science, 59*, 265-276.

King, A. J., & Cowlishaw, G. (2009). All together now: behavioural synchrony in baboons. *Animal Behaviour, 78*, 1381-1387.

King, A. J., Johnson, D. D., & van Vugt, M. (2009). The origins and evolution of leadership. *Current Biology, 19*, R911-R916.

King, A. J., Sueur, C., Huchard, E., & Cowlishaw, G. (2011). A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Animal Behaviour*, *82,* 1337-1345.

Kinzey, W. G., & Cunningham, E. P. (1994). Variability in platyrrhine social organization. *American Journal of Primatology*, 34, 185-198.

Kinzey, W. G. (1997a). *Cebus*. In W.G. Kinzey (Ed.) *New World Primates. Ecology, Evolution and Behavior* (pp.248-257). Walter de Gruyter Inc.

Kinzey, W. G. (1997b). *Saimiri.* In W.G. Kinzey (Ed.) *New World Primates. Ecology, Evolution and Behavior* (pp.297-305). Walter de Gruyter Inc.

Kleiman, D. G. (1989). Reintroduction of captive mammals for conservation. *BioScience, 39*, 152-161.

Kleiman, D. G. (1992). Behavior research in zoos: past, present, and future. *Zoo Biology, 11*, 301-312.

Kleiman, D.G., Beck, B. B., Dietz, J. M., Dietz, L. A., Ballou, J. D. & Coimbra-Filho, A. F. (1986). Conservation program for the golden lion tamarin: captive research and management, ecological studies, educational strategies, and reintroduction. In K. Benirschke (Ed.), *Primates: The road to self-sustaining populations* (pp. 959-979). Springer.

Klein, L. L., & Klein, D. J. (1973). Observations on two types of Neotropical primate intertaxa associations. *American Journal of Physical Anthropology*, *38*, 649-653.

Klein, L. L., & Klein, D. J. (1975). Social and ecological contrasts between four taxa of Neotropical primates. In R.H, Tuttle (Ed.), *Socioecology and psychology of primates* (pp. 59-85). Mouton Publishers.

Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. (2001). The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society B, 268*, 187–196.

Koontz, F. W. (1997). Zoos and *in situ* conservation. *Primate conservation: the role of zoological parks*, 63-81.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, *15*, 259-263.

Koyama, N. F. (2003). Matrilineal cohesion and social networks in *Macaca fuscata*. *International Journal of Primatology*, *24*, 797-811.

Krause, J. (1994). Differential fitness returns in relation to spatial position in groups. *Biological Reviews*, *69*, 187-206.

Krause, J., Lusseau, D., & James, R. (2009). Animal social networks: an introduction. *Behavioral Ecology and Sociobiology, 63*, 967-973.

Krause, J., & Ruxton, G. D. (2002). *Living in Groups*. Oxford University Press.

Krause, J., Croft, D. P., & James, R. (2007). Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology*, 62, 15-27.

Krebs, J. R., & Davies, N. B. (1993). *An Introduction to Behavioural Ecology*. Blackwell: Oxford.

Krebs, J. R., & Kacelnik, A. (1991). Decision-making. In: J.R. Krebs & N.B. Davies (Eds.), *Behavioural ecology: an evolutionary approach, 3rd edn* (pp. 105-136). Blackwell Scientific Publications.

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.

Kummer, H. (1957). Soziales Verhalten einer Mantelpavianen-Gruppe. *Schweizerische Zeitschrift fuer Psychologie*, *Beiheft 33*,1-91.

Kummer, H. (1968). *Social Organization of Hamadryas Baboons*. University of Chicago Press.

Kummer, H. (1971). *Primate societies: group techniques of ecological adaptation*. Aldine-Atherton.

Kummer, H. (1978). On the value of social relationships to nonhuman primates: a heuristic scheme. *Social Science Information, 17,* 687-705.

Kurland, J. A. (1975). Kin selection in Japanese macaques: evidence from kin-directed behaviours. *American Journal of Physical Anthropology, 2,* 312-313.

Kurvers, R. H., Adamczyk, V. M., Kraus, R. H., Hoffman, J. I., van Wieren, S. E., van der Jeugd, H. P., Amos, W., Prins, H. T. T., & Jonker, R. M. (2013). Contrasting context dependence of familiarity and kinship in animal social networks. *Animal Behaviour*, *86*, 993-1001.

Kutsukake, N. (2000). Matrilineal rank inheritance varies with absolute rank in Japanese macaques. *Primates*, *41*, 321-335.

Lakin, J. L., Jefferis, V. E., Cheng, C. M., & Chartrand, T. L. (2003). The chameleon effect as social glue: Evidence for the evolutionary significance of non-conscious mimicry. *Journal of Nonverbal Behaviour, 27*, 145–162.

Lambert, J. E., & Garber, P. A. (1998). Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology, 45*, 9-28.

Lamprecht, J. (1985). Distress call alternation in hand reared goslings (*Anser indicus*): vocal cooperation between siblings. *Animal Behaviour, 22*, 728-737. Cited in: King, A. J., & Cowlishaw, G. (2009). All together now: behavioural synchrony in baboons. *Animal Behaviour, 78*, 1381-1387.

Landeau, L., & Terborgh, J. (1986). Oddity and the 'confusion effect' in predation. *Animal Behaviour, 34*, 1372-1380.

Langguth. A. & Alonso, C. (1997). Capuchin monkeys in the Caatinga: tool use and food habits during drought. *Neotropical Primates, 5*, 77–78.

Latané, B., Schneider, E., Waring, P., & Zweigenhaft, R. (1971). The specificity of social attraction in rats. *Psychonomic Science, 23*, 28-29.

Lee, P. C. (1987). Nutrition, fertility and maternal investment in primates. *Journal of Zoology*, *213*, 409-422.

Lee, P. C. (1994). Social structure and evolution. In T.R. Halliday & P.J.B. Slater (Eds.), *Behaviour and evolution* (pp. 266-303). Cambridge University Press.

Lee, P. C., & Oliver, J. I. (1979). Competition, dominance and the acquisition of rank in juvenile yellow baboons (*Papio cynocephalus*). *Animal Behaviour, 27*, 576-585.

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour*, *74*, 1617-1629.

Lehmann, J., & Ross, C. (2011). Baboon (*Papio anubis*) social complexity – A network approach. *American Journal of Primatology*, *73*, 1-15.

Lehtonen, J., & Jaatinen, K. (2016). Safety in numbers: the dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology*, *70*, 449-458.

Leonardi, R., Buchanan-Smith, H. M., Dufour, V., MacDonald, C., & Whiten, A. (2010). Living together: behavior and welfare in single and mixed species groups of capuchin (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology*, *72*, 33-47.

Leutenegger, W., & Kelly, J. T. (1977). Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates, 18*, 117-136.

Levi, T., Silvius, K. M., Oliveira, L. F., Cummings, A. R., & Fragoso, J. M. (2013). Competition and facilitation in the Capuchin–Squirrel Monkey relationship. *Biotropica,45*, 636-643.

Lickliter, R., & Ness, J. W. (1990). Domestication and comparative psychology: Status and strategy. *Journal of Comparative Psychology, 104*, 211.

Lima, S. L. (1990). The influence of models interpretation of vigilance. In: Bekoff, M., Jamieson, D. (Eds.) *Interpretation and explanation in the study of animal behavior, explanation, evolution and adaption, vol 2* (pp. 246-267). Westview Press.

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*, 11-20.

Lima, M. G., Buckner, J. C., Silva ‐ Júnior, J. D. S. E., Aleixo, A., Martins, A. B., Boubli, J. P., Link, A., Farias, I. P., Nazareth da Silva, M., Röhe, F., Queiroz, H., Chiou, K. L., Di Fiore, A., Alfaro, M. E., & Lynch Alfaro, J. W. (2017). Capuchin monkey biogeography: understanding *Sapajus* Pleistocene range expansion and the current sympatry between *Cebus* and *Sapajus*. *Journal of biogeography*, *44*, 810-820.

Lima, S. L., & Zollner, P. A. (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, 11, 131-135.

Limmer, B., & Becker, P. H. (2007). The relative role of age and experience in determining variation in body mass during the early breeding career of the common tern (*Sterna hirundo*). *Behavioral Ecology and Sociobiology*, *61*, 1885-1896.

Lorge, I. (1955). Groupness of the group. *Journal of Educational Psychology, 46*, 449-456.

Louwerse, M. M., Dale, R., Bard, E. G., & Jeuniaux, P. (2012). Behavior matching in multimodal communication is synchronized. *Cognitive Science, 36,* 1404–1426.

Lusseau, D. (2007). Evidence for social role in a dolphin social network. *Evolutionary ecology, 21*, 357-366.

Lusseau, D., & Newman, M. E. (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*, S477-S481.

Lynch Alfaro, J. W. L., Silva JR, J. D. S. E., & Rylands, A. B. (2012a). How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. *American Journal of Primatology, 74*, 273-286.

Lynch Alfaro, J. W., Boubli, J. P., Olson, L. E., Di Fiore, A., Wilson, B., Gutiérrez-Espeleta, G. A., Chiou, K. I., Schulte, M., Neitzel, S., Ross, V., Schwochow, D., Nguyen, M. T. T., Farias, I., Janson, C. H., & Alfaro, M. E. (2012b). Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *Journal of biogeography, 39*, 272-288.

Lynch Alfaro, J. W. L., Boubli, J. P., Paim, F. P., Ribas, C. C., da Silva, M. N. F., Messias, M. R., Röhe, F., Mercês, M. P., Silva JR, J. S., Silva, C. R., Pinho, G. M., Koshkarian, G., Nguyen, M. T. T., Harada, M. L., Rabelo, R. M., Queiroz, H. L., Alfaro, M. E., & Farias, I. P. (2015). Biogeography of squirrel monkeys (genus *Saimiri*): South-central Amazon origin and rapid pan-Amazonian diversification of a lowland primate. *Molecular phylogenetics and evolution, 82*, 436-454.

MacCormick, H. A., MacNulty, D. R., Bosacker, A. L., Lehman, C., Bailey, A., Anthony Collins, D., & Packer, C. (2012). Male and female aggression: lessons from sex, rank, age, and injury in olive baboons. *Behavioral Ecology*, *23*, 684-691.

MacDonald, C., & Whiten, A. (2011). The 'Living Links to Human Evolution' research centre in Edinburgh zoo: a new endeavour in collaboration. *International Zoo Yearbook*, *45*, 7-17.

MacKinnon, J. R. & MacKinnon, J. S. (1980). Niche differentiation in a primate community. In D.J. Chivers (Ed.), *Malayan forest primates: ten years' study in tropical rain forest* (pp. 167-190). Plenum Press.

MacLean, E. L., Merritt, D. J., & Brannon, E. M. (2008). Social complexity predicts transitive reasoning in prosimian primates. *Animal behaviour*, *76*, 479-486.

Makagon, M. M., McCowan, B., & Mench, J. A. (2012). How can social network analysis contribute to social behavior research in applied ethology? *Applied animal behaviour science, 138*, 152-161.

Macedonia, J.M. (1986). Effects of housing differences upon activity budgets in captive sifakas (*Propithecus verreauxi*). *Zoo Biology, 6,* 55-67.

Mallapur, A., Waran, N., & Sinha, A. (2005). Use of Enclosure Space by Captive Lion-Tailed Macaques (*Macaca silenus*) Housed in Indian Zoos. *Journal of Applied Animal Welfare Science, 8*, 175-185.

Maple, T.L., & Finlay, T.W. (1986). Evaluating the environments of captive non-human primates. In: Benirschke, K. (Ed.). *Primates: The road to self-sustaining populations* (479-488pp). New York: Springer-Verlag.

Marler, P. R., & Hamilton, W. J. (1966). *Mechanisms of animal behavior*. John Wiley & Sons, Inc.

Marsh, L. K., Boubli, J., Mittermeier, R. A., Rohe, F., Urbani, B. & de Azevedo, R. (2018). *Pithecia pithecia*. The IUCN Red List of Threatened Species 2018: e.T43942A17991915. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T43942A17991915.en. Downloaded on 26 February 2020.

Marthy, W., & Farine, D. R. (2018). The potential impacts of the songbird trade on mixed-species flocking. *Biological Conservation*, *222*, 222-231.

Martin, P., & Bateson, P. P. G. (2007). *Measuring behaviour: An introductory guide*. Cambridge University Press.

Mason, G. J. (1991). Stereotypies: a critical review. *Animal behaviour, 41*, 1015-1037.

Mason, G. J., & Latham, N. (2004). Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? *Animal Welfare, 13*, S57-S69.

Mateo, J. M. (1996). The development of alarm-call response behaviour in free-living juvenile Belding's ground squirrels. *Animal Behaviour, 52,* 489-505.

McFarland, R. (1997). Female primates: fat or fit. In M.E. Morbeck, A. Galloway, & A.L. Zihlman (Eds.). *The Evolving Female: A Life History Perspective* (pp. 163-175). Princeton University Press.

McGraw, W. S. (1994). Census, habitat preference, and polyspecific associations of six monkeys in the Lomako Forest, Zaire. *American Journal of Primatology, 34*, 295–307.

McPhee, M. E. (2003a). Effects of captivity on response to a novel environment in the oldfield mouse (*Peromyscus polionotus subgriseus*). *International Journal of Comparative Psychology, 16*, 85-94.

McPhee, M. E. (2004). Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. *Biological conservation, 115*, 71-77.

McPhee, M. E. (2004). Morphological change in wild and captive oldfield mice *Peromyscus polionotus subgriseus*. *Journal of Mammalogy, 85*, 1130-1137.

McPhee, M. E., & Carlstead, K. (2010). The importance of maintaining natural behaviors in captive mammals. *Wild mammals in captivity: Principles and techniques for zoo management, 2*, 303-313.

Meise, K., Franks, D. W., & Bro-Jørgensen, J. (2019). Using social network analysis of mixed-species groups in African savannah herbivores to assess how community structure responds to environmental change. *Philosophical Transactions of the Royal Society B*, *374*, 20190009.

Melfi, V. A., & Feistner, A. T. C. (2002). A comparison of the activity budgets of wild and captive Sulawesi crested black macaques (*Macaca nigra*). *Animal Welfare*, *11*, 213-222.

Mellor, D. J. (2016). Moving beyond the "five freedoms" by updating the "five provisions" and introducing aligned "animal welfare aims". *Animals*, *6*, 59.

Mellor, D. J., & Beausoleil, N. J. (2015). Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare, 24,* 241–253.

Mellor, D. J., & Reid, C. S. W. (1994). Concepts of animal well-being and predicting the impact of procedures on experimental animals. In: *Improving the Well-being of Animals in the Research Environment. Australian and New Zealand Council for the Care of Animals in Research and Teaching* (pp. 3–18). Glen Osmond.

Mendoza, S. P., Lowe, E. L., Davidson, J. M., & Levine, S. (1978). Annual cyclicity in the squirrel monkey *(Saimiri sciureus*): The relationship between testosterone, fatting and sexual behavior. *Hormones and Behavior, 20*, 295–303.

Mercado III, E., & Frazer, L. N. (1999). Environmental constraints on sound transmission by humpback whales. *The Journal of the Acoustical Society of America*, *106*, 3004-3016.

Mercado III, E. (2016). Acoustic signaling by singing humpback whales (*Megaptera novaeangliae*): what role does reverberation play? *PLoS ONE 11*, e0167277.

Mitani, M. (1991). Niche overlap and polyspecific associations among sympatric cercopithecids in the Campo Animal Reserve, southwestern Cameroon. *Primates, 32*, 137-151.

Mittermeier, R. A., & van Roosmalen, M. G. M. (1981). Preliminary observations on habitat utilization and diet in eight Surinam monkeys. *Folia Primatologica, 36*, 1-39.

Mittermeier, R. A. & Rylands, A. B. (2018). *Cebus olivaceus*. The IUCN Red List of Threatened Species 2018: e.T43941A17981329. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T43941A17981329.en. Downloaded on 28 July 2020.

Mittermeier, R. A., Rylands, A. B. & Boubli, J. (2018). *Saguinus midas*. The IUCN Red List of Threatened Species 2018: e.T41525A17932579. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T41525A17932579.en. Downloaded on 28 July 2020.

Mittermeier, R. A., Rylands, A. B. & Boubli, J. (2019). *Ateles paniscus*. *The IUCN Red List of Threatened Species* 2019: https://dx.doi.org/10.2305/IUCN.UK.2019-2.RLTS.T2283A17929494.en. Downloaded on 28 July 2020.

Moermond, T. C. (1979). Habitat constraints on the behavior, morphology, and community structure of Anolis lizards. *Ecology*, *60*, 152-164.

Morrell, L. J., Ruxton, G. D., & James, R. (2011). Spatial positioning in the selfish herd. *Behavioral Ecology*, *22*, 16-22.

Morse, D. H. (1977). Feeding behavior and predator avoidance in heterospecific groups. *Bioscience, 27*, 332– 339.

Morton, F. B. (2014). Individual differences in learning, personality and social success in brown capuchin monkeys (*Sapajus apella*) [Unpublished doctoral thesis]. The University of Stirling, Scotland.

Moura, A. D. A., & Lee, P. C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science, 306,* 1909.

Moynihan, M. (1976). *The new world primates.* Princeton: Princeton University Press.

Nakamura, M. (1997). First observed case of chimpanzee predation on yellow baboons (*Papio cynocephalus*) at the Mahale mountains national park. *Pan Africa News,* 9-11.

Nekaris, K. A. I., Liyanage, W. K., & Gamage, S. N. (2005). Influence of forest structure and composition on population density of the red slender loris *Loris tardigradus tardigradus* in Masmullah proposed forest reserve, Sri Lanka. *Mammalia, 69*, 201-210.

Newton, P. N. (1989). Associations between langur monkeys (*Presbytis entellus*) and chital deer (*Axis axis*): chance encounters or a mutualism? *Ethology, 83*, 89-120.

Newton-Fisher, N. E. (2017). Modeling social dominance: Elo-ratings, prior history, and the intensity of aggression. *International journal of primatology, 38*, 427-447.

Noë, R., & Bshary, R. (1997). The formation of red colobus–Diana monkey associations under predation pressure from chimpanzees. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *264*, 253-259.

Nonaka, E., & Holme, P. (2007). Agent-based model approach to optimal foraging in heterogeneous landscapes: effects of patch clumpiness. *Ecography*, *30*, 777-788.

Norconk, M. A. (1986). *Interactions between primate species in a neotropical forest: mixed species troops of* Saguinus mystax *and* S. fuscicollis *(Callitrichidae),* [Unpublished PhD thesis]. The University of California.

Norconk, M. A., & Kinzey, W. G. (1994). Challenge of Neotropical frugivory: travel patterns of spider monkeys and bearded sakis. *Americna Journal of Primatology, 34*, 171-183.

Norconk, M. A., Grafton, B. W., & Conklin ‐ Brittain, N. L. (1998). Seed dispersal by neotropical seed predators. *American Journal of Primatology, 45*, 103-126.

Nuttall, D. B. (2004). An animal-as-client (AAC) theory for zoo exhibit design. *Landscape research*, *29*, 75-96.

Nurmohamed, R., Naipal, S., & Becker, C. (2007). Rainfall variability in Suriname and its relationship with the tropical Pacific ENSO SST anomalies and the Atlantic SST anomalies. *International Journal of Climatology, 27*, 249-256.

O'Brien, T. G. (1991). Female-male social interactions in wedge-capped capuchin monkeys: benefits and costs of group living. *Animal Behaviour, 41*, 555-567.

O'Neill, P.L. (1994). Expression of species-specific behavior in rhesus monkeys. *Lab Animal, 23,* 40-44.

Oates, J. F., & Whitesides, G. H. (1990). Association between olive colobus (*Procolobus versus*), Diana guenons (*Cercopithecus diana*), and other forest monkeys in Sierra Leone. *American Journal of Primatology, 21*, 129–146.

Oda, R., & Masataka, N. (1996). Interspecific responses of ringtailed lemurs to playback of antipredator alarm calls given by Verreaux's sifakas. *Ethology*, *102*, 441-453.

Ödberg, F. (1978). Introduction to abnormal behaviour: stereotypies. In *Proceedings of the 1st World Congress on Ethology Applied to Zootechnics* (pp. 475-480). Industrias Graficas.

Ogden, J.J., Finlay, T.W., & Maple, T.L. (1990). Gorilla adaptations to naturalistic environments. *Zoo Biology, 9,* 107-121.

Olupot, W., Chapman, C. A., Waser, P. M., & Isabirye–Basuta, G. (1997). Mangabey (*Cercocebus albigena*) Ranging Patterns in Relation to Fruit Availability and the Risk of Parasite Infection in Kibale National Park, Uganda. *American Journal of Primatology, 43*, 65-78.

Packer, C., & Pusey, A. E. (1979). Female aggression and male membership in troops of Japanese macaques and olive baboons. *Folia primatologica*, *31*, 212-218.

Pannozzo, P. L., Phillips, K. A., Haas, M. E., & Mintz, E. M. (2007). Social monitoring reflects dominance relationships in a small captive group of brown capuchin monkeys (*Cebus apella*). *Ethology*, *113*, 881-888.

Parga, J. A., & Overdorff, D. J. (2011). Primate socioecology. In C. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder, & R.M. Stumpf (Eds.), *Primates in perspective* (pp. 12-18). New York: Oxford University Press.

Parnell, R. J. (2002). Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *American Journal of Primatology, 56*, 193-206.

Parr, L. A., Matheson, M. D., Bernstein, I. S., & de Waal, F. B. M. (1997). Grooming down the hierarchy: allogrooming in captive brown capuchin monkeys, *Cebus apella. Animal Behaviour, 54*, 361-367.

Parrish, J. K., & Hamner, W. M. (1997). *Animal groups in three dimensions: how species aggregate.* Cambridge: Cambridge University Press.

Partridge, B. L. (1981). Internal dynamics and the interrelations of fish in schools. *Journal of comparative physiology, 144,* 313-325.

Partridge, B. L. (1982). The structure and function of fish schools. *Scientific American, 246,* 114-123.

Pasquaretta, C., Levé, M., Claidière, N., van De Waal, E., Whiten, A., MacIntosh, A. J. J., Pelé, M., Bergstrom, M. L., Borgeaud, C., Brosnan, S. F., Crofoot, M. C., Fedigan, L. M., Fichtel, C., Hopper, L. M., Mareno, M. C., Petit, O., Schnoell, A. V., Polizzi di Sorrentino, E., Thierry, B., Tiddi, B., & Sueur, C. (2014). Social networks in primates: smart and tolerant species have more efficient networks. *Scientific reports, 4*, 7600.

Paukner, A., Anderson, J. R., Borelli, E., Visalberghi, E., & Ferrari, P. F. (2005). Macaques (*Macaca nemestrina*) recognize when they are being imitated. *Biology Letters*, *1*, 219-222.

Paulk, H.H., Dienske, H., & Ribbens, L.G. (1977). Abnormal behaviour in relation to cage size in rhesus monkeys. *Journal of Abnormal Psychology, 86,* 87–92.

Pays, O., Ekori, A., & Fritz, H. (2014). On the advantages of mixed-species groups: impalas adjust their vigilance when associated with larger prey herbivores. *Ethology, 120*, 1207-1216.

Pays, O., Goulard, M., Blomberg, S. P., Goldizen, A. W., Sirot, E., & Jarman, P. J. (2009). The effect of social facilitation on vigilance in the eastern gray kangaroo, *Macropus giganteus. Behavioral Ecology, 20*, 469-477.

Peet, R. K. (1974). The measurement of species diversity. *Annual review of ecology and systematics*, *5,* 285-307.

Peperpot Nature Park. (2017, December 12). The protected Peperpot nature reserve in the district of Commewijne, Suriname: Press Message. Retrieved from http://www.bosenbos.nl/wp-content/uploads/2013/10/persbericht-wwf-peperpot-nature-park-ceremonie-updated-final-1.pdf

Pereira, A. S., Rebelo, I. D., Cassanova, C., Lee, P. C., & Louca, V. (2020). The multidimensionality of female mandrill sociality – A dynamic multiplex network. *PLoS ONE, 15*, e0230942.

Peres, C. A. (1992). Prey-capture benefits in a mixed-species group of Amazonian tamarins, *Saguinus fuscicollis* and *S. mystax*. *Behavioral Ecology and Sociobiology, 31*, 339-347.

Peres, C. (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 tamarins (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins in Amazonian *terra firme* forest. *Journal of Zoology, 23*, 567-592.

Perry, S., Manson, J. H., Dower, G., & Wikberg, E. (2003). White-faced capuchins cooperate to rescue a groupmate from a *Boa constrictor*. *Folia Primatologica*, *74*, 109-111.

Perry, S., Barrett, H. C., & Manson, J. H. (2004). White-faced capuchin monkeys show triadic awareness in their choice of allies. *Animal Behaviour, 67*, 165–170.

Perry, S., Manson, J. H., Muniz, L., Gros-Louis, J., & Vigilant, L. (2008). Kin-biased social behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. *Animal Behaviour*, *76*, 187-199.

Petit, O., Gautrais, J., Leca, J. B., Theraulaz, G., & Deneubourg, J. L. (2009). Collective decision-making in white-faced capuchin monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *276(1672)*, 3495-3503.

Pettifor, R. A. (1990). The effects of avian mobbing on a potential predator, the European kestrel, Falco tinnunculus. *Animal Behaviour*, *39*, 821-827.

Pinheiro, T., Ferrari, S. F., & Lopes, M. A. (2011). Polyspecific associations between squirrel monkeys (*Saimiri sciureus*) and other primates in eastern Amazonia. *American journal of primatology, 73*, 1145-1151.

Pitcher, T. J., Magurran, A. E., & Allan, J. R. (1983). Shifts of behaviour with shoal size in cyprinids. *Proceedings of the 3rd British Freshwater Fisheries Conference, 3*, 220-221.

Plowman, A. B. (2003). A note on a modification of the spread of participation index allowing for unequal zones. *Applied Animal Behaviour Science, 83*, 331-336.

Podolsky, R. D. (1990). Effects of mixed-species association on resource use by *Saimiri sciureus* and *Cebus apella*. *American Journal of Primatology*, *21*, 147-158.

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.

Poole, T. B. (1991). Criteria for the provision of captive environments. In *Primate responses to environmental change* (pp. 357-374). London: Chapman and Hall.

Powell, G. V. N. (1985). Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. *Ornithological Monographs, 36*, 713-732.

Prescott, M. J. (1999). Social learning in mixed-species troops of *Saguinus fuscicollis* and *Saguinus labiatus*: tests of foraging benefit hypotheses in captivity [unpublished PhD thesis]. The University of Stirling.

Prescott, M. J. & Buchanan-Smith, H. M. (2004). Cage sizes for tamarins in the laboratory. *Animal Welfare, 13*, 151-158.

Price, E. O. (1984). Behavioral aspects of animal domestication. *The quarterly review of biology, 59*, 1-32.

Price, E. O. (1998). Behavior genetics and the process of animal domestication. In: T. Grandin, (Ed.), *Genetics and the Behavior of Domestic Animals* (pp. 31–65). Academic Press.

Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology, 38,* 419–422.

Pulliam, H. R. (1976). The principle of optimal behavior and the theory of communities. In P.P.G. Bateson & P.H. Klopfer (Eds.). *Perspectives in ethology* (pp. 311-332). Springer.

Pulliam, H. R., Pyke, G. H. & Caraco, T. (1982). The scanning behaviour of juncos: a game theoretical approach. *Journal of Theoretical Biology, 95*, 89–103.

Pulliam, H. R. & Caraco, T. (1984). Living in groups: is there an optimal group size? In (Eds.) C.J. Krebs & N.B. Davies. *Behavioural Ecology*, (pp. 122–147). Sinauer.

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL https://www.r-project.org/.

Raghoenandan, U. P. D. (2000). The Guianas (Guyana, Suriname, French Guiana). In *Inselbergs* (pp. 315-338). Springer Berlin.

Ramos-Fernández, G., Boyer, D., Aureli, F., & Vick, L. G. (2009). Association networks in spider monkeys (*Ateles geoffroyi*). *Behavioral Ecology and Sociobiology*, *63*, 999-1013.

Ramseyer, F., & Tschacher, W. (2006). Synchrony: A core concept for a constructivist approach to psychotherapy. *Constructivism in the Human Sciences*, 11, 150–171. Cited in: Duranton, C., & Gaunet, F. (2016). Behavioural synchronization from an ethological perspective: overview of its adaptive value. *Adaptive Behavior*, *24,* 181-191.

Rands, S. A., Cowlishaw, G., Pettifor, R. A., Rowcliffe, J. M. & Johnstone, R. A. (2008). The emergence of leaders and followers in foraging pairs when the qualities of individuals differ. *BMC Evolutionary Biology*, 8, 51.

Rasa, O. A. (1987). The dwarf mongoose: a study of behaviour and social structure in relation to ecology in a small social carnivore. *Advances in the Study of Behavior, 17*,121–163.

Reade, L. S., & Waran, N. K. (1996). The modern zoo: How do people perceive zoo animals? *Applied Animal Behaviour Science, 47*, 109-118.

Rees, P. A. (2011). *An introduction to zoo biology and management*. John Wiley & Sons.

Reinhardt, V., & Liss, C., & Stevens, C. (1996). Space requirement stipulations for caged non-human primates in the United States: A critical review. *Animal Welfare, 5*, 361-372.

Rice, D. W. (1956). Dynamics of range expansion of Cattle Egrets in Florida. *The Auk, 73*, 259-266.

Ricklefs, R., & Relyea, R. (2014). *Ecology: The economy of nature (7th ed.)*. W. H. Freeman.

Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal behaviour*, *51*, 1077-1086.

Roberts, J. Y., & Quintard, B. (2009). *European Stud Book (Guianan Brown Capuchin* Cebus apella apella*)*. Besancon.

Robinson, J. (1981). Spatial structure in foraging groups of wedge-capped capuchin monkeys (*Cebus nigrivittatus*). *Animal Behaviour*, *29*, 1036-1056.

Rodman, P. S. (1978). Diets, densities and distributions of Bornean primates. In: Montgomery, G. G. (ed.). *Ecology of Arboreal Folivores* (pp. 465–478). Washington DC: Smithsonian Institute Press.

Rodman, P. S. (1981). Inclusive fitness and group size with a reconsideration of group sizes in lions and wolves. *The American Naturalist*, *118*, 275-283.

Rodman, P. S., & Mitani, J. C. (1987). Orang-utans: sexual dimorhism in a solitary species. In eds. B. Smuts, D., Cheney, R., Seyfarth, R., Wrangham, & T., Struhsaker (Eds.). *Primate Societies* (pp.146–154). University of Chicago Press.

Rodríguez–Gironés, M. A., & Vasquez, R. A. (2002). Evolutionary stability of vigilance coordination among social foragers. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269(1502),* 1803-1810.

Rook, A. J., & Penning, P. D. (1991). Synchronisation of eating, ruminating and idling activity by grazing sheep. *Applied Animal Behaviour Science, 32*, 157-166.

Rose, L. M. (1994). Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology, 15*, 95-114.

Rose, L. M., & Fedigan, L. M. (1995). Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Animal Behaviour*, *49*, 63-70.

Rose, P. E., & Croft, D. P. (2015). The potential of Social Network Analysis as a tool for the management of zoo animals. *Animal Welfare*, 24, 123-138.

Rosenberger, A. L. (1980). Gradistic views and adaptive radiation of platyrrhine primates. *Zeitschrift für Morphologie und Anthropologie*, *71,* 157-163.

Rosenberger, A. L. (1981). Systematics: the higher taxa. *Ecology and Behavior of Neotropical Primates, 1*, 9-27.

Ross, C. (1993). Predator mobbing by an all-male band of hanuman langurs (*Presbytis entellus*). *Primates, 34*, 105–107.

Ross, R. A., & Giller, P. S. (1988). Observations on the activity patterns and social interactions of a captive group of blackcapped or brown capuchin monkeys (*Cebus apella*). *Primates*, *29*, 307-317.

Ross, S. R., & Lukas, K. E. (2006). Use of space in a non-naturalistic environment by chimpanzees (*Pan troglodytes*) and lowland gorillas (*Gorilla gorilla gorilla*). *Applied Animal Behaviour Science*, *96*, 143-152.

Ross, S. R., Schapiro, S. J., Hau, J., & Lukas, K. E. (2009). Space use as an indicator of enclosure appropriateness: A novel measure of captive animal welfare. *Applied Animal Behaviour Science, 121*, 42-50.

Ross, S.R., Calcutt, S., Schapiro, S.J., & Hau, J. (2011). Space use selectivity by chimpanzees and gorillas in an indoor-outdoor enclosure. *American Journal of Primatology, 73*, 197-208.

Rowell, T. (1972). *The social behaviour of monkeys*. Penguin Books, Harmondsworth.

Rowell, T. E., & Hinde, R. A. (1962). Vocal communication by the rhesus monkey (*Macaca mulatta*). In *Proceedings of the Zoological Society of London* (Vol. 138, No. 2, pp. 279-294). Blackwell Publishing Ltd.

Rubenstein, D. I. (1978). On predation, competition, and the advantages of group living. In P. Bateson & P. Klopfer (Eds.), *Perspectives in ethology* (pp. 205-230). Plenum Press.

Ruckstuhl, K. E. (1998). Foraging behaviour and sexual segregation in bighorn sheep. *Animal behaviour*, *56*, 99-106.

Ruckstuhl, K. E. (1999). To synchronise or not to synchronise: a dilemma for young bighorn males? *Behaviour*, *136,* 805.

Ruckstuhl, K. E., & Kokko, H. (2002). Modelling sexual segregation in ungulates: effects of group size, activity budgets and synchrony. *Animal Behaviour*, *64*, 909-914.

Rudran, R. (1977). Socioecology of the blue monkey (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest, Uganda. *Smithsonian Contributions to Zoology, 249*, 1-88.

Rusticus, S. A., & Lovato, C. Y. (2014). Impact of sample size and variability on the power and type I error rates of equivalence tests: A simulation study. *Practical Assessment, Research, and Evaluation*, *19*, 1-10.

Ruxton, G. D., Hall, S. J., & Gurney, W. S. C. (1995). Attraction toward feeding conspecifics when food patches are exhaustible. *The American Naturalist*, *145*, 653-660.

RStudio Team. (2020). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Rylands, A. B., Schneider, H., Langguth, A., Mittermeier, R. A., Groves, C. P., & Rodríguez-Luna, E. (2000). An assessment of the diversity of new world primates. *Neotropical Primates, 8*, 61-93.

Rylands, A. B., & Mittermeier, R. A. (2013). Family Cebidae (squirrel monkeys and capuchins). In R.A., Mittermeier, A.B., Rylands, & D.E., Wilson (Eds.). *Handbook of the Mammals of the World. Vol 3. Primates* (pp. 348-413). Lynx Edicions

Sade, D. S. (1965). Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. *American Journal of Physical Anthropology, 23*, 1-17

Sade, D. S. (1972). Sociometrics of *Macaca mulatta* I. Linkages and Cliques in Grooming Matrices. *Folia Primatologica, 18*, 196-223.

Sade, D. S. (1989). Sociometrics of *Macaca mulatta* III: N-path centrality in grooming networks. *Social Networks*, *11*, 273-292.

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour, 62*, 265-271.

Schino, G., Giuseppe, F., Visalberghi, E. (2009). Grooming, rank, and agonistic support in tufted capuchin monkeys. *American Journal of Primatology, 71*,101-105.

Schmitt, M. H., Stears, K., Wilmers, C. C., & Shrader, A. M. (2014). Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds. *Animal Behaviour, 96,* 151-158.

Schoener, T. W. (1988). Ecological interactions. In A.A. Myers & P.S. Giller (Eds.). *Analytical Biogeography* (pp. 255-297). Chapman & Hall.

Scott, J. (2000). *Social network analysis: A handbook.* SAGE Publications Ltd.

Scott, J. (2013). *Social network analysis* (3rd ed.). SAGE Publications Ltd.

Seyfarth, R., & Cheney, D. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behaviour*, *40*, 754-764.0

Shelden, K. E. W., Baldridge, A. & Withrow, D. E. (1995). Observations of Risso's dolphins *Grampus griseus* with gray whales *Eschrichtius robustus*. *Marine Mammal Science, 11*, 231–240.

Shultz, S., & Dunbar, R. I. (2007). The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 2429-2436.

Sibly, R. M. (1983). Optimal group size is unstable. *Animal Behaviour, 31,* 947–948.

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology*, 63, 975-988.

Silk, J. B. (2002). Kin selection in primates. *International Journal of Primatology, 23,* 849–875.

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, *302*, 1231-1234.

Silk, J. B., Alberts, S. C., & Altmann, J. (2004). Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour*, *67*, 573-582.

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Shapiro, S. (2013). Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal behaviour, 85*, 941-947.

Silva, J. S. Jr. (2001). Especiação nos macacos-prego e caiararas, gênero *Cebus* Erxleben, 1777 (Primates, Cebidae), [Unpublished PhD Thesis]. Universidade Federal do Rio de Janeiro.

Smith, A. C. (1997). Comparative Ecology of Saddle-Back (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*) tamarins, [Unpublished PhD Thesis]. University of Reading.

Smith, A. C., Buchanan-Smith, H. M., Surridge, A. K., & Mundy, N. I. (2005). Factors affecting group spread within wild mixed-species troops of saddleback and mustached tamarins. *International Journal of Primatology, 26*, 337-355.

Smith, J. E. (2014). Hamilton's legacy: kinship, cooperation and social tolerance in mammalian groups. *Animal Behaviour, 92*, 291-304.

Smith, J. M., & Szathmáry, E. (1995). *The major transitions in evolution* (pp. 255-278). Oxford University Press.

Snaith, T. V., & Chapman, C. A. (2005). Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Piliocolobus tephrosceles*). *Behavioral Ecology and Sociobiology*, *59*, 185-190.

Sodaro, V. (1999). Housing and exhibiting mixed species of neotropical primates. In N., Saunders & V., Sodaro (eds.). *Callitrichid husbandry manual* (pp 7-34). Neotropical Primate Taxon Advisory Group.

Sosa, S. (2016). The influence of gender, age, matriline and hierarchical rank on individual social position, role and interactional patterns in *Macaca Sylvanus* at 'la forêt des singes': A multilevel social network approach. *Frontiers in Psychology, 7*, 529.

Southwick, C. H., & Southwick, K. L. (1983). Polyspecific groups of macaques on the Kowloon peninsula, New Territories, Hong Kong. *American Journal of Primatology*, *5*, 17-24.

Stankowich, T. (2003). Marginal predation methodologies and the importance of predator preferences. *Animal Behaviour, 66,* 589-599.

Stanley, C. R., & Dunbar, R. I. M. (2013). Consistent social structure and optimal clique size revealed by social network analysis of feral goats, *Capra hircus. Animal Behaviour, 85*, 771-779.

Stensland, E. V. A., Angerbjörn, A., & Berggren, P. E. R. (2003). Mixed species groups in mammals. *Mammal Review, 33*, 205-223.

Stewart, K. J. & Harcourt, A. H. (1994). Gorilla's vocalisations during rest periods: signals of impending departure? *Behaviour 130*, 29–40

Stoinski, T. S., Hoff, M. P., & Maple, T. L. (2000). Habitat Use and Structural Preferences of Captive Western Lowland Gorillas (*Gorilla gorilla gorilla*): Effects of Environmental and Social Variables. *International Journal of Primatology, 22*, 431-445.

Stokke, S., & du Toit, J. T. (2000). Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography*, *23*, 70-80.

Stone, A. I. (2014). Is fatter sexier? Reproductive strategies of male squirrel monkeys (*Saimiri sciureus*). *International Journal of Primatology, 35*, 628-642.

Strayer, F. F., Bovenkerk, A., & Koopman, R. F. (1975). Social affiliation and dominance in captive squirrel monkeys (*Saimiri sciureus*). *Journal of Comparative and Physiological Psychology, 89*, 308.

Strier, K. B. (1997). Subtle cues of social relations in male muriqui monkeys (*Brachyteles arachnoides*). In W.G. Kinzey (Ed.), *New world primates: Ecology, evolution, and behaviour* (pp. 109-126). Walter de Gruyter Inc.

Strier, K. B. (1999). Why is female kin bonding so rare? Comparative sociality of neotropical primates. In P.C. Lee (Ed.). *Comparative Primate Socioecology* (pp. 300-319). Cambridge University Press.

Strier K. (2007). *Primate Behavioural Ecology* (3rd ed). USA: Pearson Education Inc.

Strier, K. B., & Mendes, S. L. (2009). Long-term field studies of South American primates. In P.A. Garber, A. Estrada, J.C. Bicca-Marques, E.W. Heymann & K.B. Strier (Eds.). *South American Primates*, (pp. 139-155). Springer.

Struhsaker, T. T. (1970). Phylogenetic implications of some vocalizations of Cercopithecus monkeys. In Napier, J. R., & Napier, P. H. (Eds.), *Old World Monkeys* (pp. 367-444.). Academic 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, Behaviour* (pp. 225-248). Academic Press.

Struhsaker, T. T. (1981). Polyspecific associations among tropical rain-forest primates. *Zeitschrift für Tierpsychologie, 57*, 268-304.

Stueckle, S., & Zinner, D. (2008). To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. *Animal Behaviour*, *75,* 1995-2004.

Suchi, S., & Rothe, H. (1999). The influence of abiotic factors on the onset and cessation of activity of semi-free *Callithrix jacchus*. *American Journal of Primatology 47*, 241-253.

Sueur, C., & Petit, O. (2008). Organization of group members at departure is driven by social structure in Macaca. *International Journal of Primatology*, *29*, 1085-1098.

Sueur, C., Petit, O., & Deneubourg, J. L. (2009). Selective mimetism at departure in collective movements of *Macaca tonkeana*: an experimental and theoretical approach. *Animal Behaviour*, *78,* 1087-1095.

Sueur, C., Jacobs, A., Amblard, F., Petit, O., & King, A. J. (2011). How can social network analysis improve the study of primate behavior? *American journal of primatology, 73,* 703-719.

Sueur, C., Deneubourg, J. L., & Petit, O. (2012). From social network (centralized vs. decentralized) to collective decision-making (unshared vs. shared consensus). *PLoS one*, *7,* e32566.

Sumpter, D. J. (2010). *Collective animal behavior*. Princeton University Press.

Sundaresan, S. R., Fischhoff, I. R., Dushoff, J., & Rubenstein, D. I. (2007). Network metrics reveal differences in social organization between two fission–fusion species, Grevy's zebra and onager. *Oecologia, 151*, 140-149.

Suriname Conservation Foundation (SCF). (2012). *Central Suriname nature reserve – a pristine treasure*. Suriname Conservation Foundation.

Sussman, R. W. (2000). Cebidae. In RW, Sussman (Ed.) *Primate Ecology and Social Structure* (pp.69-124). Pearson Custom Publishing.

Sussman, R.W. (2003). *Primate Ecology and Social Structure. Volume 2: New World Monkeys, Revised First Edition*. Pearson Custom Publishing.

Sutherland, W. J. (1996). *From individual behaviour to population ecology* (Vol. 11). Oxford University Press.

Sutherland, W. J. (2006). *Ecological census techniques: a handbook*. Cambridge University Press.

Symons, D. (1978). *Play and aggression: A study of rhesus monkeys*. Columbia University Press.

Teelen, S. (2007). Influence of chimpanzee predation on associations between red colobus and red-tailed monkeys at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology, 28*, 593-606.

Tello, N. S., Huck, M., Heymann, E. W. (2002). *Boa constrictor* attack and successful group defence in moustached tamarins, *Saguinus mystax*. *Folia Primatologica, 73*, 146-148.

Terborgh, J. (1983). *Five new world primates: a study in comparative ecology* (pp. 156-189). Princeton 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.

Thomas, W. D. & Maruska, E. J. (1996). Mixed species exhibits with mammals. In D.G. Kleiman, M.E. Allen, K.V. Thompson & S. Lumpkin (Eds.), *Wild Mammals in Captivity: Principles and Techniques* (pp. 204-211). University of Chicago Press.

Thompson, D. B. A., & Barnard, C. J. (1983). Anti-predator responses in mixed-species associations of lapwings, golden plovers and black-headed gulls. *Animal Behaviour, 31*, 585-593.

Thorington, R. W. (1967). Feeding and activity in *Cebus* & *Saimiri* in a Colombian forest. In D., Starck, R., Schneider, & H.J., Kuhn (eds.). *Progress in Primatology: First congress of the international primatological society* (pp 180-184). Gustav Fischer Verlag.

Thorndike, R. L., & Stein, S. (1937). An evaluation of the attempts to measure social intelligence. *Psychological Bulletin, 34,* 275.

Thorpe, W. H., & Zangwill, O. L. (1961). *Current problems in animal behaviour*. Cambridge University Press.

Tiddi, B., Aureli, F., & Schino, G. (2010). Grooming for infant handling in tufted capuchin monkeys: a reappraisal of the primate infant market. *Animal Behaviour*, *79*, 1115-1123.

Tiddi, B., Aureli, F., Schino, G., & Voelkl, B. (2011). Social relationships between adult females and the alpha male in wild tufted capuchin monkeys. *American journal of primatology*, *73*, 812-820.

Tiddi, B., Aureli, F. & Schino, G. (2012). Grooming up the hierarchy: the exchange of grooming and rank-related benefits in a new world primate. *PLoS one, 7,* e36641.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für tierpsychologie*, *20*, 410-433.

Tinbergen, N. (1974). *Curious naturalists*. University of Massachusetts Press.

Tokunaga, D. H., & Mitchell, G. (1977). Factors affecting sex differences in nonhuman primate grooming. *Journal of Behavioural Science, 2*, 259–269.

Traylor-Holzer, K., & Fritz, P. (1985). Utilization of space by adult and juvenile groups of captive chimpanzees (*Pan troglodytes*). *Zoo Biology*, *4*, 115-127.

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. II. An economic model for predator-prey interaction. *Animal Behaviour, 23*, 801-825.

Treves, A. (1999). Within-group vigilance in red colobus and redtail monkeys. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *48*, 113-126.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.) *Sexual Selection & the Descent of Man* (pp. 136-179). Aldine Publishing Company.

Turner, G. F., & Pitcher, T. J. (1986). Attack abatement: a model for group protection by combined avoidance and dilution. *The American Naturalist*, *128*, 228-240.

Tyack, P. (1982). Humpback whales respond to sounds of their neighbours [Unpublished doctoral thesis]. Rockefeller University.

UNESCO. (2017a, November 26). Central Suriname nature reserve. Retrieved from http://whc.unesco.org/en/list/1017

UNESCO. (2017b, November 26). Central Suriname nature reserve – WHC Nomination Report. Retrieved from http://whc.unesco.org/uploads/nominations/1017.pdf

Vahl, W. K., Van Der Meer, J., Meijer, K., Piersma, T., & Weissing, F. J. (2007). Interference competition, the spatial distribution of food and free-living foragers. *Animal Behaviour*, *74*, 1493-1503.

van Belle, S., Estrada, A., & Garber, P. A. (2013). Collective group movement and leadership in wild black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology*, *67*, 31-41.

van Roosmalen, M. G. M. (1985). *Fruits of the Guianan flora*. Institute of Systematic Botany, Utrecht University, Netherlands.

van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour, 87*, 120-144.

van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates*, *40*, 69-86.

van Schaik, C. P., & van Hooff, J. A. R. A. M. (1983). On the ultimate causes of primate social systems. *Behaviour*, *85*, 91-117.

Vermeer, J. (2006). Husbandry Guidelines for Squirrel Monkeys (genus *Saimiri*). *European Association of Zoos and Aquariums Document*. Romagne, France: La Vallée des Singes.

Vine, I. (1971). Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology, 30*, 405-422.

Viscido, S. V., & Shrestha, S. (2015). Using quantitative methods of determining group membership to draw biological conclusions. *Animal Behaviour*, *104*, 145-154.

Visalberghi, E. (1987). Acquisition of nut-cracking behaviour by 2 capuchin monkeys (*Cebus apella*). *Folia Primatologica*, *49*, 168-181.

Vogel, E. R. (2005). Rank differences in energy intake rates in white-faced capuchin monkeys, *Cebus capucinus*: the effects of contest competition. *Behavioral ecology and sociobiology*, *58*, 333-344.

von Frisch, K. (1967). *The dance language and orientation of bees*. Harvard University Press.

Wang, X., Sun, L., Li, J., Xia, D., Sun, B., & Zhang, D. (2015). Collective movement in the Tibetan macaques (*Macaca thibetana*): Early joiners write the rule of the game. *PLoS One, 10*, e0127459 1-14.

Ward, A. & Webster, M. (2016). *Sociality: behaviour of group-living animals.* Switzerland: Springer International Publishing.

Waser, P. M. (1974). *Intergroup interaction in a forest monkey: The mangabey, Cercocebus albigena* [Unpublished doctoral thesis]. Rockefeller University.

Waser, P. M. (1980). Polyspecific associations of *Cercocebus albigena*: geographic variation and ecological correlates. *Folia Primatologica, 33*, 57-76.

Waser, P. M. (1982). Primate polyspecific associations: do they occur by chance? *Animal Behaviour*, *30*, 1-8.

Waser, P. M. (1984). “Chance” and mixed-species associations. *Behavioral Ecology and Sociobiology, 15*, 197-202.

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). University of Chicago Press.

Wasserman, S., & Faust, K. (1994). *Social network analysis methods and applications*. Cambridge University Press.

Weinbaum, K., Nzooh, Z., Usongo, L., & Laituri, M. (2007). Preliminary survey of forest elephant crossings in Sangha Trinational Park, central Africa. *Pachyderm*, *43*, 52-61.

Wells, J. P., & Turnquist, J. E. (2001). Ontogeny of locomotion in rhesus macaques (*Macca mulatta*): II. Postural and locomotor behavior and habitat use in a free-ranging colony. *American of Physical Anthropology, 115*, 80-94.

West, S. A., Griffin, A. S., & Gardner, A. (2007). Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of evolutionary biology*, *20*, 415-432.

Wey, T., Blumstein, D. T., Shen, W., & Jordan, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal behaviour, 75,* 333-344.

White, L. J. T., & Edwards, A. (2000). Methods for assessing the status of animal populations. In L. J. T. White and A. Edwards (Eds.). *Conservation research in the African rain forest: A technical handbook.* Wildlife Conservation Society, New York.

Whitehead, H. (1997). Analysing animal social structure. *Animal behaviour, 53*, 1053-1067.

Whitehead, H. (1999). Testing association patterns of social animals. *Animal Behaviour, 57*, F26–F29.

Whitehead, H. (2008). *Analyzing animal societies: quantitative methods for vertebrate social analysis*. University of Chicago Press.

Whitehead, H. (2009). SOCPROG programs: analyzing animal social structures. *Behavioral Ecology and Sociobiology*, 63, 765-778

Whiten, A., & Byrne, R. W. (1988a). The Machiavellian intelligence hypothesis: editorial. In A. Whiten & R.W. Byrne (Eds.), *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans* (pp.1-9). Oxford University Press.

Whiten, A., & Byrne, R. W. (1988b). Tactical deception in primates. *Behavioral and brain sciences, 11*, 233-244.

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. *Advances in the Study of Behavior,21*, 239–283.

Whitesides, G. H. (1989). Interspecific association of diana monkeys, *Ceropithecus diana*, in Sierra Leone, West Africa: biological significance or chance? *Animal Behaviour, 37*, 760-776.

Williams, R., & Lusseau, D. (2006). A killer whale social network is vulnerable to targeted removals. *Biology letters, 2*, 497-500.

Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Harvard University Press.

Wing, L. (1946). Species association in winter groups. *The Auk, 63*, 508-511.

Winn, L. K., & Winn, H. E. (1985). *Wings in the sea; the humpback whale*. University Press of New England.

Wittemyer, G., Douglas-Hamilton, I., & Getz, W. M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal behaviour, 69*, 1357-1371.

World Conservation Union, IUCN. (1987). The IUCN policy statement of captive breeding. Gland, Switzerland. In F. W. Koontz. (1997). Zoos and *in situ* primate conservation. *American Society of Primatologists, 1,* 63-81.

Wrangham, R. W. (1979). On the evolution of ape social systems. *Information (International Social Science Council)*, *18*, 336-368.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, *75*, 262-300.

Wrangham, R. W. (1983). Social relationships in comparative perspective. In R.A. Hinde & C.M. Berman (Eds.). *Primate social relationships: An integrated approach* (pp. 325-334). Blackwell Scientific Publications.

Wrangham, R. W. (1987). Evolution of social structure. In R.A. Hinde (Ed.), *Primate social relationships: an integrated approach* (pp. 255-262). Blackwell Scientific Publications.

Wrangham, R. W. & Rubenstein, D. I. (1986). Social evolution in birds and mammals. In D. I. Rubenstein & R. W. Wrangham (Eds.), *Ecological Aspects of Social Evolution* (pp. 352-378). Princeton University Press.

Wrangham, R. W., Gittleman, J. L. & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day range as assays of exploitation competition. *Behavioral Ecology and Sociobiology, 32*, 199-209.

WWF. (2017, December 10). WWF Guianas Highlights. Retrieved from http://d2ouvy59p0dg6k.cloudfront.net/downloads/highlights_2014_final_web.pdf

Yoneda, M. (1984). Comparative studies on vertical separation, foraging behavior and traveling mode of saddle-backed tamarins (*Saguinus fuscicollis*) and red-chested moustached tamarins (*Saguinus labiatus*) in northern Bolivia. *Primates, 25,* 414-422.

Zaeschmar, J. R., Dwyer, S. L., & Stockin, K. A. (2013). Rare observations of false killer whales (*Pseudorca crassidens*) cooperatively feeding with common bottlenose dolphins (*Tursiops truncatus*) in the Hauraki Gulf, New Zealand. *Marine Mammal Science*, *29*, 555-562.

Zemel, A., & Lubin, Y. (1995). Inter-group competition and stable group sizes. *Animal Behaviour*, *50*, 485-488.

Zhang, P., Li, B. G., Qi, X. G., MacIntosh, A. J., & Watanabe, K. (2012). A proximity-based social network of a group of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). *International Journal of Primatology*, *33*, 1081-1095.

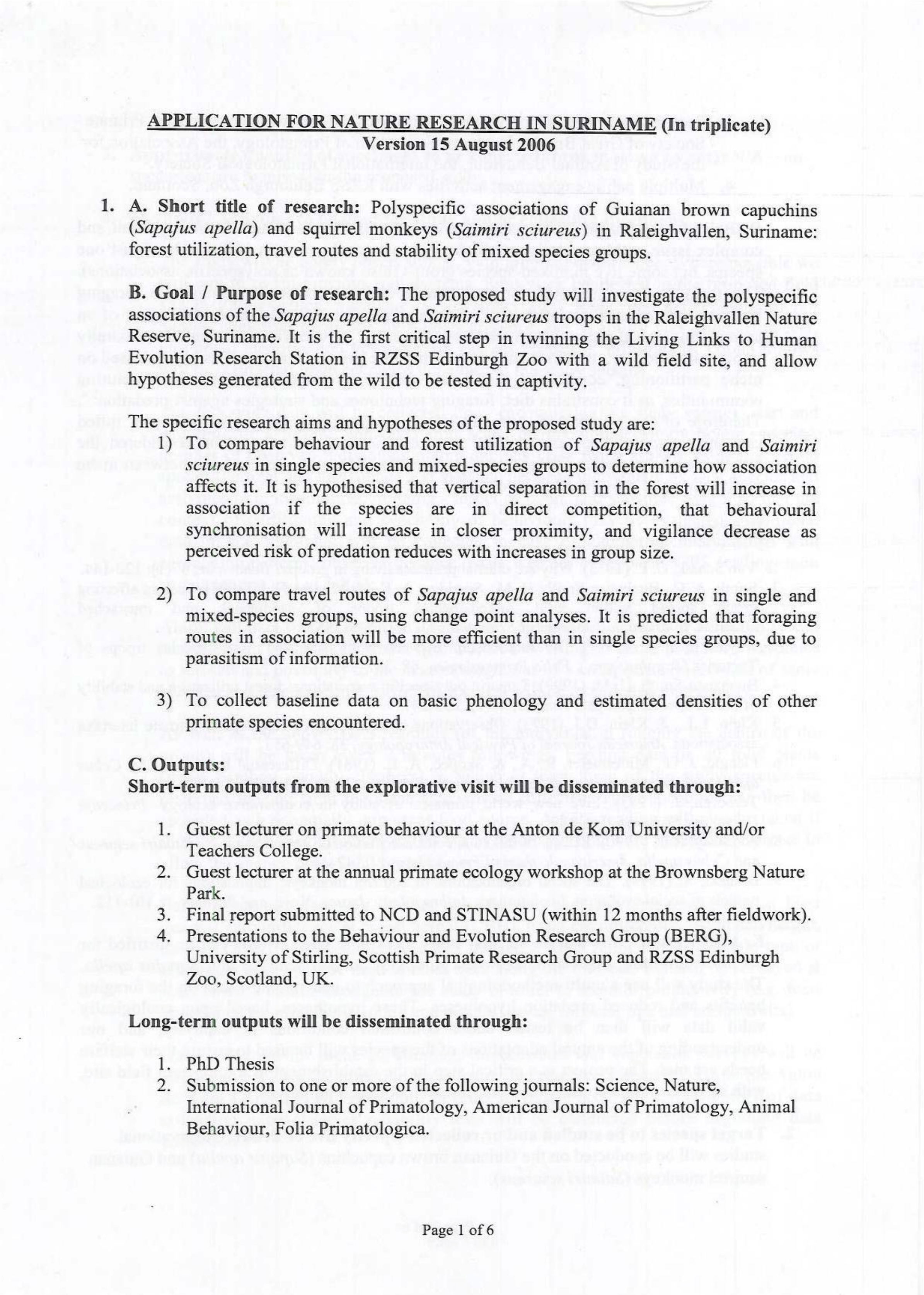
Zimbler-DeLorenzo, H. S., & Stone, A. I. (2011). Integration of field and captive studies for understanding the behavioral ecology of the squirrel monkey (*Saimiri* sp.). *American Journal of Primatology, 73*, 607-622.

Zuberbühler, K. (2000a). Interspecies semantic communication in two forest primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*, 713-718.

Zuberbühler, K. (2000b). Interspecies semantic communication in two forest primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 267*, 713-718.

9 APPENDICES

Appendix I. *Permits for fieldwork at Raleighvallen and Peperpot*



APPLICATION FOR NATURE RESEARCH IN SURINAME (In triplicate)

Version 15 August 2006

1. **A. Short title of research:** Polyspecific associations of Guianan brown capuchins (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) in Raleighvallen, Suriname: forest utilization, travel routes and stability of mixed species groups.

B. Goal / Purpose of research: The proposed study will investigate the polyspecific associations of the *Sapajus apella* and *Saimiri sciureus* troops in the Raleighvallen Nature Reserve, Suriname. It is the first critical step in twinning the Living Links to Human Evolution Research Station in RZSS Edinburgh Zoo with a wild field site, and allow hypotheses generated from the wild to be tested in captivity.

The specific research aims and hypotheses of the proposed study are:

1) To compare behaviour and forest utilization of *Sapajus apella* and *Saimiri sciureus* in single species and mixed-species groups to determine how association affects it. It is hypothesised that vertical separation in the forest will increase in association if the species are in direct competition, that behavioural synchronisation will increase in closer proximity, and vigilance decrease as perceived risk of predation reduces with increases in group size.

2) To compare travel routes of *Sapajus apella* and *Saimiri sciureus* in single and mixed-species groups, using change point analyses. It is predicted that foraging routes in association will be more efficient than in single species groups, due to parasitism of information.

3) To collect baseline data on basic phenology and estimated densities of other primate species encountered.

C. Outputs:

Short-term outputs from the explorative visit will be disseminated through:

1. Guest lecturer on primate behaviour at the Anton de Kom University and/or Teachers College.
2. Guest lecturer at the annual primate ecology workshop at the Brownsberg Nature Park.
3. Final report submitted to NCD and STINASU (within 12 months after fieldwork).
4. Presentations to the Behaviour and Evolution Research Group (BERG), University of Stirling, Scottish Primate Research Group and RZSS Edinburgh Zoo, Scotland, UK.

Long-term outputs will be disseminated through:

1. PhD Thesis
2. Submission to one or more of the following journals: Science, Nature, International Journal of Primatology, American Journal of Primatology, Animal Behaviour, Folia Primatologica.

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3. Posters and/or presentations at one or more of the following conferences: Primate Society of Great Britain, European Federation of Primatology, the Association for the Study of Animal Behaviour, the International Primatological Society.
4. Multiple public engagement activities with RZSS Edinburgh Zoo, Scotland.

D. Brief background: Understanding why animals live in groups is an important and complex issue within evolutionary biology. Most groups contain individuals of just one species, but some live in mixed-species groups (also known as polyspecific associations). The main reasons proposed for both single and mixed-species groups are foraging benefits and reduced predation risk[1]. Spatial ecology is another important aspect of an animal's biological repertoire, in terms of where it is in its environment and its proximity to other individuals[2]. Previous studies on sympatric primate communities has focussed on niche partitioning, concluding that body size is an important factor in structuring communities, as it constrains diet, foraging techniques and strategies against predation[3,4]. Therefore of the Neotropical primates known to form polyspecific associations, tufted capuchins *Sapajus* spp. and squirrel monkeys *Saimiri* spp. should be considered the opportune study species for research intending to address the relationship between niche partitioning and polyspecific association[5,6,7,8,9].

References

1. Van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour*, 87(1): 120-144.
2. Smith, A. C., Buchanan-Smith, H. M., Surridge, A. K., & Mundy, N. I. (2005). Factors affecting group spread within wild mixed-species troops of saddleback and mustached tamarins. *International Journal of Primatology*, *26*(2): 337-355.
3. Heymann, E.W. (1997) The relationship between body size and mixed-species troops of Tamarins (*Saguinus* spp.). *Folia Primatologica*, 68: 287–295.
4. Buchanan-Smith, H. M. (1999). Tamarin polyspecific associations: forest utilization and stability of mixed-species groups. *Primates*, 40(1): 233-247.
5. Klein, L.L., & Klein, D.J. (1973). Observations on two types of Neotropical primate intertaxa associations. *American Journal of Physical Anthropology*, 38: 649-653.
6. Fleagle, J. G., Mittermeier, R. A., & Skopec, A. L. (1981). Differential habitat use by *Cebus apella* and *Saimiri sciureus* in central Surinam. *Primates*, *22*(3), 361-367.
7. Terborgh, J. (1983). Five new world primates: A study in comparative ecology. *Princeton University Press*. pp. 156-189.
8. Podolsky, R.D. (1990). Effects of mixed-species association on resource use by *Saimiri sciureus* and *Cebus apella*. *American Journal of Primatology*, 21:147–158.
9. Boinski, S. (1999). The social organizations of squirrel monkeys: implications for ecological models of social evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 8: 101-112.

E. Justification: This will be the first study to explore what criteria can be justified for use in determining association between groups of *Saimiri sciureus* and *Sapajus apella*. The study will use a multi-methodological approach to generate new data on the foraging benefits and reduced predation hypotheses. These hypotheses, based upon ecologically valid data will then be tested under controlled conditions in captivity, and our understanding of the natural adaptations of the species will be used to ensure their welfare needs are met. The project is a critical step in the establishment of a long-term field site, with its concomitant conservation and research outreach initiatives.

2. **Target species to be studied and/or collected (specify live or dead):** Observational studies will be conducted on the Guianan brown capuchins (*Sapajus apella*) and Guianan squirrel monkeys (*Saimiri sciureus*).

3. **Approximate quantity of specimens to be collected (broken down by sex):** N/A – no specimens are required for the proposed study.

4. **Methods / Activities to be used for study and/or collecting specimens.**

The study will be purely observational, with minimal disturbance. Where possible we will aim to re-cut previous trail systems. Pilot work conducted at the proposed field site in Raleighvallen, Suriname in November 2015 found that neither *Sapajus* nor *Saimiri* appeared perturbed by human presence and visibility was good. However, individual identification beyond basic age sex classes is not possible. Group follows will be conducted upon encountering either of the study species.

The following data will be collected upon encountering the study species: start and end time of a follow, and on 5 min scans on maximum canopy height, species, number of observed individuals noting age sex class when known, estimated group spread (vertical and horizontal) and distance between individuals of each species and activities (e.g. locomotion, foraging - insect or plant, and substrate usage) so that the context of partitioning and synchrony of behaviours may be evaluated. Additional data on the following will be collected in case of alternative relationships with association patterns: observer distance, basic weather description, GPS reading upon encounter and end of follow.

Alarm call data will be recorded *ad libitum,* noting the species, their height in forest, and direction of the likely threat (ground, tree dwelling or aerial predator). Response to the call and proximity to the nearest neighbour of a conspecific (individual of same species) and heterospecific (different species) will be recorded systematically.

As well as the above, GPS readings (of the individual at roughly the centre of the group) will be taken every 2 minutes following[1]. Feeding data on all food plants (trees, bamboo, woody climbers) in which at least three of the study species are observed feeding from the same tree will be collected. These locations can then be recorded as a potentially important food source. A GPS reading will also be taken if there is a change in direction of travel and where possible note the leading species to allow the change point analyses to be performed.

Basic phenology data (e.g. habitat classification and structure, species [or at least genera], circumference at breast height [CBH], basal circumference, estimated height, canopy cover) will be collected along transects. Tags (either biodegradable tape or aluminum tags[2]) will be used to label trees along the transect, and will be surveyed at least twice a month throughout the study in order to monitor productivity (e.g. food abundance for primates – young and mature leaves, flowers, ripe and unripe fruits).

Data collection for niche partitioning, travel routes and vegetation surveys will be alternated between the principle investigator and research assistant(s) (from the Anton de Kom University of Suriname). In order to ensure accuracy and reliability of data collection, inter-observer reliability tests will be conducted before beginning data collection[3].

All the work abides by the Association for the Study of Animal Behaviour Ethical Guidelines[4], and the study has been approved by the Psychology Ethics Committee at the University of Stirling, Scotland.

References

1. Asensio, N., Brockelman, W., Malaivijitnond, S., & Reichard ,U. (2011). Gibbon travel paths are goal oriented. *Animal Cognition*, 14:395–405.
2. Ganzhorn, J., Rackotondranary, S.J., & Ratovonamana, Y.R. (2003). Habitat description and phenology. In Setchell, J.M., & Curtis, D.J. (eds.), *Field and Laboratory Methods in Primatology* (pp. 40-56). Cambridge University Press.
3. Martin, P., & Bateson, P. P. G. (2007). Measuring behaviour: an introductory guide. *Cambridge University Press*. 176p.
4. A.S.A.B. (2012). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour*, 83: 301–309.

5. **Localities where research and/or collecting is to take place:** The Raleighvallen Nature Reserve – around the existing Voltzberg trail and Sue Boinski's old site (04° 42.955'N, 056° 12.660'W).

6. **A. Time required for permit (max. 12 months, subject to review for renewal):** 12 months maximum (September 2016-August 2017).

B. Time schedule of outputs / activities:
September 2016
Flight from the UK to Suriname.
Complete Visa requirements.
Meeting with STINASU/NCD and contact field assistant(s) and field guide(s) to finalise paper work and confirm logistics to Raleighvallen.
Purchase field supplies.

September/October 2016 – August 2017
Travel to the Raleighvallen.
Training research/field assistants.
Trail cutting and phenology data collection.
Habituation and pilot data collection.
Data collection.
Participate in the Primate workshop(s) at the Brownsberg Nature Reserve.
Guest lecture on primate research at the Anton de Kom University.

August 2017
Travel back to Paramaribo.
A presentation shall be held and a short written summary (hard copy and electronic copy) of the most important aspects of the research shall be submitted to NCD before departure from Suriname.
Flight from Suriname to the UK.

2018
A preliminary report (hard copy and electronic copy) of results of work completed under the permit will be submitted to NCD and STINASU within 12 months after completion of fieldwork.
Final reports, publications, checklists, maps, slides/pictures and other relevant documentation/ material pertinent to the fieldwork (x 3 hard copies and x3 electronic copies) shall be given free of charge to NCD and STINASU with permission for non-primarily commercial use.
Dissemination of results to the Living Links to Human Evolution Research Centre at the Royal Zoological Society Scotland's (RZSS) Edinburgh Zoo.
Present at one or more of the following conferences: Scottish Primate Research Group, European Federation of Primatology and the Primate Society of Great Britain, RZSS Edinburgh Zoo Summer conference, International Primatological Society.

2019
Presentation or poster the Primate Society of Great Britain spring meeting.
Submit PhD thesis.
Prepare manuscripts for submission to various journal articles (see 1C Outputs).

7. **Supporting documents from universities, major professors, and/or institutions:** See attached letters of support from the Head of Psychology Professor David Donaldson and from my PhD Supervisor Professor Hannah Buchanan-Smith.

8. **Source of funds and total research budget:** Submitted applications to the following –
The Leakey Foundation
The Nacey Maggioncalda Foundation
The Primate Society of Great Britain
The Conservation International - Primate Action Fund
Rufford Small Grants

In the event of any of the above applications being unsuccessful, or pitfalls in funding the Principle Investigator will cover costs by their own means.

9. **Names and address(es) of Applicant, participating Officials and / or Assistants:**

Name – Miss Sophia Daoudi (PhD Student, Principle Investigator)
Address – Psychology
School of Natural Sciences
The University of Stirling
Stirling
FK9 4LA
UK

Name – Arioené Vreedzaam (Project Coordinator)
Address – United Nations House - SGP
Gonggrijpstraat 25
Paramaribo
Suriname

Research Assistants – to be confirmed
Recruiting Research Assistants from the Anton de Kom University, Suriname.

10. **Address(es) of institutes where specimens will be stored (established research collection):** N/A – no specimens are required for the proposed study.

11. **The available donation in cash or in kind (e.g. goods and/or technical assistance) for management – including related research, education and awareness) of protected areas and / or wildlife:**

    Our contribution will be to enhance the research skills of Surinamese students in primate ecology and biodiversity, both theoretical as well as practical and where possible, we will contribute to park management in relation to biodiversity conservation.

12. **The Applicant agrees with the attached General Regulations for Nature Research in Suriname:** See attached.

13. **Attachments:**

    A. **General Regulations for Nature Research on species of Wild Fauna and Flora in Suriname.**
    B. **Curriculum Vitae of Applicant and participating Officials and / or Assistants.**
    C. **Written confirmation of the Director of the institute (s) where the specimens will be stored. (see point 10)** – N/A no specimens are required for the proposed study.

Application Date : 16-MAY-2016

Applicant's Name : SOPHIA DAOUDI

Applicant's Signature :

Paramaribo, 20 juni 2016
Approved on behalf of the Head of Suriname Forest Service,

Head of the Nature Conservation Division,

Note:

1. If necessary, this information can be given on one or more separate sheets.
2. In case you will stay longer than three months in Suriname, it will be necessary to take a certificate of good character with you.

PEPERPOT
NATURE PARK

From: **Foundation "Peperpot Nature Park"**
Commewijne, Meerzorg
Telephone: (+597) 354547

November 10, 2017

To whom it may concern,

Sophia Daoudi has been working with us for a few months starting since May 2017 and express her interest in a project on the monkeys of Peperpot Nature Park.

Being a researcher, she observed monkey species within the Mopentibo area, and gathered data on the species of monkeys and their behaviour.

Her collected data is valued and will be used in further student projects and by our education and tourism crew, to share the gained knowledge with our visistors. Our park management will also consider to use the collected data to help in the conservation of the monkey species at Mopentibo.

I herewith, classify Sophia Daoudi as an excited and skilled field researcher

Sincerely,

Serano Ramcharan MSc.
Research Coordinator Peperpot Nature Park

Appendix II. *Ethical approval for fieldwork*

PSYCHOLOGY DIVISION ETHICAL APPROVAL FORM

Check one box: ☐ STAFF project ☐ UNDERGRADUATE project ☒ POSTGRADUATE project
Title of project: Polyspecific associations of Guianan brown capuchins (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) in Raleighvallen, Suriname: forest utilization, travel routes and stability of mixed species groups.
Name of Researcher(s) Sophia Daoudi
Email Address s.m.daoudi1@stir.ac.uk
Name of Supervisor(s) (for student research) Prof. Hannah Buchanan-Smith
Date 20th July 2016

Postgraduate and Staff Projects

Please indicate your source of funding (Division, Research Council, Govt, Charity, etc)
Self-funded PhD, application under review for funding from Primate Action Fund (charity) and Rufford Small Grants (charity)

		Yes	No	N/A
1	Will you tell participants that their participation is voluntary?	☐	☐	☒
2	Will you tell participants that they may withdraw at any time and for any reason?	☐	☐	☒
3	Will you obtain written consent for participation?	☐	☐	☒
4	Will you tell participants that their data will be treated with full confidentiality and that, if published, it will not be identifiable as theirs?	☐	☐	☒
5	If an experiment, will you describe the main experimental procedures to participants in advance, so that they are informed about what to expect?	☐	☐	☒
6	With questionnaires, will you give participants the option of omitting any questions they do not want to answer?	☐	☐	☒
7	If the research is observational, will you ask participants for their consent to being observed?	☐	☐	☒
8	Will you debrief participants at the end of their participation (i.e. give them a brief explanation of the study)?	☐	☐	☒

If you have ticked **No** to any of Q1-8, you should normally **tick box B** overleaf; if not, please give an explanation on a separate sheet.. [Note: N/A = not applicable]

			Yes	No	N/A
9	Will your project involve deliberately misleading participants in any way?		☐	☐	☒
10	Is there any realistic risk of you or any participants experiencing either physical or psychological discomfort, distress or harm?		☐	☒	☐
11	Will you be administering drugs or other substances to your participants, or taking fluid or other samples from them?		☐	☒	☐
12	Does your project involve work with animals?		☒	☐	☐
13	Do participants fall into any of the following special groups? If they do please refer to BPS guidelines, and **tick box B** overleaf. Note that you may also need to obtain satisfactory CRB clearance (or equivalent for overseas students)	Schoolchildren (under 18yrs)	☐	☒	☐
		People with learning or communication difficulties	☐	☒	☐
		Patients	☐	☒	☐
		People in custody	☐	☒	☐
		People engaged in illegal activities (e.g. drug taking)	☐	☒	☐

If you have ticked **Yes** to any of Q9 - 13 you should normally **tick box B** overleaf; if not, please give an explanation on a separate sheet.

DECLARATION

I am familiar with the BPS Guidelines for ethical practices in psychological research. I understand that there is an obligation on the lead researcher to bring to the attention of the Ethics Committee any issues with ethical implications not clearly covered by the checklist.

Please tick to confirm: ☒

PLEASE TICK **EITHER** BOX A OR BOX B BELOW AND **PROVIDE THE DETAILS REQUIRED** IN SUPPORT OF YOUR APPLICATION.

B. I consider that this project **may** have ethical implications that should be brought before the Division committee, and/or it will be carried out with children or other vulnerable populations	☒
Please provide details on a separate sheet.	
Checklist for a Part B submission:-	**Please tick**
• Project title	☒
• Purpose of project and its academic rationale	☒
• Number of participants (age, gender, exclusion/inclusion criteria) and how they will be recruited	☐
• Start and end dates	☒
• Brief description of methods and measurements	☒
○ Where participants will be tested	☐
○ How materials will be administered	☐
○ Any novel questions or questionnaires are included with submission	☐
○ Length of time for each participant	☐
• Information/ consent form attached	☐
○ Participant allowed to withdraw at any time	☐
○ All individual data will be confidential	☐
• Debriefing form attached	☐
• A clear but concise statement of ethical considerations raised by the project and how you intend to deal with them.	☒

This form should be submitted by email to the Psychology Ethics Committee for consideration (psychethicssubs@stir.ac.uk). Please include the name of the applicant in the 'Subject' line of the email. Students should send the form to their supervisor who, after checking it, will forward it to the Psychology Ethics Committee.

Title of project

Polyspecific associations of Guianan brown capuchins (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) in Raleighvallen, Suriname: forest utilization, travel routes and stability of mixed species groups.

Purpose of project and its academic rationale

Of the eight sympatric primate species in the Raleighvallen Nature Reserve, we know that mixed-species associations are formed between *Sapajus apella* and *Saimiri sciureus* (Terborgh, 1983; Fleagle, Mittermeier & Skopec, 1981; Podolsky, 1990; Pinheiro, Ferrari & Lopes, 2011; Levi et al., 2013; Frechette, Sieving & Boinski, 2014). The phenomenon of mixed species, or polyspecific groups is particularly interesting as there is still much that we do not understand regarding their functions and proximate mechanisms for establishing and maintaining associations (Stensland, Anderbjörn & Berggren, 2003).

The proposed study will explore what criteria can be justified for use in determining association between groups of *Saimiri sciureus* and *Sapajus apella*. The study will use a multi-methodological approach to generate new data on the foraging benefits and reduced predation hypotheses. These hypotheses, based upon ecologically valid data will then be tested under controlled conditions in captivity, and our understanding of the natural adaptations of the species will be used to ensure their welfare needs are met. The project is a critical step in twinning the Living Links to Human Evolution Research Station in RZSS Edinburgh Zoo with a wild field site.

The specific research aims and hypotheses of the proposed study are:

1) To compare behaviour and forest utilization of *Sapajus apella* and *Saimiri sciureus* in single species and mixed-species groups to determine how association affects it. It is hypothesised that vertical separation in the forest will increase in association if the species are in direct competition, that behavioural synchronisation will increase in closer proximity, and vigilance decrease as perceived risk of predation reduces with increases in group size.

2) To compare travel routes of *Sapajus apella* and *Saimiri sciureus* in single and mixed-species groups, using change point analyses. It is predicted that foraging routes in association will be more efficient than in single species groups, due to parasitism of information.

3) To collect baseline data on forest structure, basic phenology and estimated densities of other primate species encountered.

Participants/Study species

Wild troop(s) of Guianan brown capuchins (*Sapajus apella*) and Guianan squirrel monkeys (*Saimiri sciureus*) at the Raleighvallen Nature Reserve, Suriname.

Start and end dates

October 2016 – September 2017

Brief Description of methods and measurements

Primate data collection

The following data will be collected upon encountering the study species: start and end time of a follow, and on 5 min scans on maximum canopy height, species, number of observed individuals noting age sex class when known, estimated group spread (vertical and horizontal) and distance between individuals of each species and activities (e.g. locomotion, foraging - insect or plant, and substrate usage) so that the context of partitioning and synchrony of behaviours may be evaluated. Additional data on the following will be collected in case of alternative relationships with association patterns: observer distance, basic weather description, GPS reading upon encounter and end of follow.

Alarm call data will be recorded *ad libitum,* noting the species, their height in forest, and direction of the likely threat (ground, tree dwelling or aerial predator). Response to the call and proximity to the nearest neighbour of a conspecific (individual of same species) and heterospecific (different species) will be recorded systematically.

As well as the above, GPS readings (of the individual at roughly the centre of the group) will be taken every 2 minutes following (Asensio, Brockelman, Malaivijitnond, & Reichard, 2011). Feeding data on all food plants (trees, bamboo, woody climbers) in which at least three of the study species are observed feeding from the same tree will be collected. These locations can then be recorded as a potentially important food source. A GPS reading will also be taken if there is a change in direction of travel and where possible note the leading species to allow the change point analyses to be performed.

Vegetation data collection

Basic phenology data (e.g. habitat classification and structure, species [or at least genera], circumference at breast height [CBH], basal circumference, estimated height, canopy cover) will be collected along transects. Tags - either biodegradable tape or aluminium tags- (Ganzhorn, Rackotondranary, & Ratovonamana, 2003) will be used to label trees along the transect, and will be surveyed at least twice a month throughout the study in order to monitor productivity (e.g. food abundance for primates – young and mature leaves, flowers, ripe and unripe fruits).

Ethical considerations raised by the project

Being purely observational, the study will involve no manipulations or invasive procedures (e.g. capturing and tagging). Furthermore, tourists and other researchers have previously visited the area, so additional researcher presence should have a minimal negative impact on the study subjects. However, it is important to consider the effects of habituation, which is when study subjects are aware of an observer's presence but have learned to ignore/tolerate them (Williamson & Feistner, 2003). Therefore, it is important to consider how wild populations of primates may be affected by habituation. For instance their tolerance towards human presence may make them more susceptible to hunting and closer proximity with humans may increase risks of disease transmission.

Fortunately, the study area is currently unaffected by anthropogenic activities such as logging, hunting, mining and settlement, and remains in pristine condition (UNESCO, 2015). However, previous research has been conducted in Raleighvallen and eco-tourism is prevalent throughout the year, so it is unlikely that additional observer presence for this study will have a negative impact on the study subjects and other sympatric species. That being said, in order to further minimise disturbance, researchers, where possible, will avoid making loud noises, sudden gestures or surreptitious movements (Williamson & Feistner, 2003). In order to minimise the risk of disease transmission, if a researcher is feeling unwell, they will not undertake any observational work and in general where possible researchers will keep at a distance, whilst maintaining good visibility of the study subjects (Williamson & Feistner, 2003).

For the most part we will be utilising existing trails, however, as some areas have not been used for a number of years, it may be necessary to cut back some of the surrounding foliage that has re-grown. This will be done with advice from a local guide and following advice from an experienced local researcher.

A full risk assessment has been completed (and approved), which includes measures to avoid any negative impact on the local people and environment. For example, any rubbish/waste from the campsite will be taken away at the end of the study.

References

Asensio, N., Brockelman, W., Malaivijitnond, S., & Reichard ,U. (2011). Gibbon travel paths are goal oriented. *Animal Cognition*, 14:395–405.

Barnett, A. (1995). Expedition field techniques: primates. Expedition Advisory Committee, Royal Geographic Society, London, UK. p85.

Fleagle, J.G., Mittermeier, R.A., & Skopec, A.L. (1981). Differential habitat use by *Cebus apella* and *Saimiri sciureus* in central Suriname. *Primates*, *22*: 361-367.

Frechette, J. L., Sieving, K. E., & Boinski, S. (2014). Social and personal information use by squirrel monkeys in assessing predation risk. *American Journal of Primatology,* 76: 956-966.

Ganzhorn, J., Rackotondranary, S.J., & Ratovonamana, Y.R. (2003). Habitat description and phenology. In Setchell, J.M., & Curtis, D.J. (eds.), *Field and Laboratory Methods in Primatology* (pp. 40-56). Cambridge University Press.

Levi, T., Silvius, K. M., Oliveira, L. F., Cummings, A. R., & Fragoso, J. (2013). Competition and facilitation in the capuchin–squirrel monkey relationship. *Biotropica*, 45:636-643.

Pinheiro, T., Ferrari, S. F., & Lopes, M. A. (2011). Polyspecific associations between squirrel monkeys (*Saimiri sciureus*) and other primates in eastern Amazonia. *American Journal of Primatology*, 73:1145-1151.

Podolsky, R.D. (1990). Effects of mixed-species association on resource use by *Saimiri sciureus* and *Cebus apella*. *American Journal of Primatology,* 21:147–158.

Stensland, E., Angerbjörn, A., & Berggren, P. (2003). Mixed species groups in mammals. *Mammal Review*, 33: 205-223.

Terborgh, J. (1983). Five New World Primates: A Study in Comparative Ecology. *Princeton University Press.* 260p.

UNESCO. (2015). Central Suriname Nature Reserve. Retrieved 26th May 2015 from: http://whc.unesco.org/en/list/1017

Williamson, E. A., & Feistner, A. T. (2003). Habituating primates: processes, techniques, variables and ethics. In: Setchell, J.M. & Curtis, D.J. (Eds.), *Field and laboratory methods in primatology: A practical guide. Cambridge University Press* pp. 25-39.

Ethical approval email

Re: Sophia Daoudi
Psychology Ethics Submissions
Wed 27/07/2016 10:15
To:Hannah Buchanan-Smith <h.m.buchanan-smith@stir.ac.uk>; Sophia Daoudi <s.m.daoudi1@stir.ac.uk>;
Cc:Psychology Ethics Submissions <psychethicssubs@stir.ac.uk>;
Dear Sophia,
Thank you for your submission for ethics.
Your project has been approved by the Psychology Ethics Committee.
Kind regards,
Lindsay

On 20 Jul 2016, at 21:12, Hannah Buchanan-Smith <h.m.buchanan-smith@stir.ac.uk> wrote:

Please find attached an ethics form for PhD student Sophia Daoudi.

This is a purely observational study, in the field in Suriname, and Sophia has carefully considered ethical implications on both study species and the environment.

Best, Hannah

Hannah M. Buchanan-Smith
Professor, Behaviour and Evolution Research Group (BERG)

Psychology, Faculty of Natural Sciences
University of Stirling
Stirling, FK9 4LA
Scotland
Tel: 01786 467674
Fax: 01786 467641
E-mail: h.m.buchanan-smith@stir.ac.uk
Home page: https://rms.stir.ac.uk/converis-stirling/person/11925

http://marmosetcare.com/
http://www.247animalwelfare.eu/index.html
Just launched: http://refiningdogcare.com/
http://www.refiningdogcare.com/images/RDC%20Flyer.pdf

<S.Daoudi(1524611)_EthicsForm-Jul2016 (1).doc>

Appendix III. *Pedigree Tables of* Sapajus *and* Saimiri *at Living Links*

Table 9.1 *West* Sapajus *demographics.*

Name	D.O.B	Sex	Dam	Sire	Origin
Diablo^D	~1971*	M	Unknown	Unknown	French Guyana
Lana	02.10.1995	F	Unknown	Chef	Besançon
Santiago	08.01.2002	F	Lana	Maurice	Paris Zoo
Diego	22.07.2002	M	Mamie	Diablo	Besançon
Sylvania	17.08.2003	F	Lana	Maurice	Paris Zoo
Toka	29.12.2004	M	Lana	Maurice	Paris Zoo
Figo	01.06.2006	M	Lana	Maurice	Edinburgh Zoo
Pedra	16.02.2008	F	Lana	Maurice	Edinburgh Zoo
Mekoe	23.04.2008	M	Sylvania	Mauirce	Edinburgh Zoo
Inti	07.09.2009	M	Sylvania	Diablo	Living Links
Rufo	21.10.2009	M	Lana	Diablo	Living Links
Ximo	02.02.2010	M	Santiago	Diablo	Living Links
Torres	08.01.2011	M	Sylvania	Diablo	Living Links
Luna	02.05.2011	F	Lana	Diablo/Diego	Living Links
Alba	18.09.2011	F	Santiago	Diablo/Diego	Living Links
Mr Fudge	14.07.2013	M	Lana	Diego	Living Links
Bear	27.07.2013	M	Santiago	Diego	Living Links
Hazel	02.09.2013	F	Sylvania	Diego	Living Links
Pixie	08.09.2013	F	Pedra	Diego	Living Links

^{D}=Deceased

* Diablo was wild born and as such the D.O.B is an approximation

Table 9.2 *East* Sapajus *demographics.*

Name	D.O.B	Sex	Mother	Father	Origin
Maurice^D	~1971*	M	Unknown	Unknown	French Guyana
Anita	14.11.1997	F	Mamie	Chef	Besançon
Junon	22.06.2000	F	Josephine	Maurice	Paris Zoo
Popeye	07.08.2001	M	Josephine	Maurice	Paris Zoo
Manuel	13.01.2004	M	Anita	Diablo	Besançon
Kato	?.08.2005	M	Unknown	Unknown	French Guyana
Penelope	20.11.2005	F	Anita	Diablo	Besançon
Carlos	22.07.2006	M	Junon	Maurice	Edinburgh Zoo
Chico	25.04.2009	M	Junon	Maurice	Living Links
Rosa	20.05.2010	F	Anita	Popeye/Maurice	Living Links
Reuben	17.05.2010	M	Junon	Popeye/Maurice	Living Links
Sol	29.07.2010	F	Penelope	Popeye	Living Links
Flojo	19.06.2011	M	Anita	Popeye	Living Links
Lindo	11.07.2011	F	Penelope	Popeye	Living Links
Willow	26.09.2012	F	Anita	Popeye	Living Links
Nena	30.12.2012	F	Penelope	Popeye	Living Links
Gustavo	31.01.2014	M	Penelope	Popeye	Living Links
Agnes	15.04.2014	F	Anita	Popeye	Living Links

^{D}=Deceased

* Maurice was wild born and as such the D.O.B is an approximation

Table 9.3 *West* Saimiri *demographics.*

Name	**D.O.B**	**Sex**	**Dam**	**Sire**	**Origin**
Hugo	20.08.10	M	Unknown	Unknown	Unknown
Gerda	05.10.99	F	Scheila	Unknown	Halle Zoo, Germany
Jasmin	14.10.02	F	Scheila	Oliver	Halle Zoo, Germany
Toomi	20.09.06	F	Jasmin	Rio	Edinburgh Zoo
Dita	09.11.09	F	Gerda	Rio	Edinburgh Zoo
Sancha	10.11.09	F	Jasmin	Rio	Edinburgh Zoo
Orla	02.11.11	F	Gerda	Rio	Edinburgh Zoo
Gisele	03.08.12	F	Gerda	Rio	Edinburgh Zoo
Loki	28.06.14	F	Jasmin	Hugo	Edinburgh Zoo

Table 9. 4 *East* Saimiri *demographics.*

Name	**D.O.B**	**Sex**	**Dam**	**Sire**	**Origin**
Boa	26.11.2005	M	301-wild born	309-wild born	Colchester Zoo
Tatu	17.04.2001	F	Unknown	304-wild born	Colchester Zoo
Roca	31.01.2003	F	Unknown	304-wild born	Colchester Zoo
Maya	26.11.2003	F	307-wild born	304-wild born	Colchester Zoo
Elie	11.11.2005	F	Unknown	304-wild born	Colchester Zoo
Cali	01.11.2005	F	Unknown	304-wild born	Colchester Zoo
Pica	26.11.2007	F	Roca	Boa	Edinburgh Zoo
Yendi	02.11.2008	F	Maya	Boa	Edinburgh Zoo
Flora	21.11.2008	F	Elie	Boa	Edinburgh Zoo
Sipi	25.12.2009	F	Verde^D	Boa	Edinburgh Zoo
Lexi	26.10.2010	F	Elie	Boa	Edinburgh Zoo
Dora	30.11.2010	F	Verde^D	Boa	Edinburgh Zoo
Amarilla	09.11.2011	F	Elie	Boa	Edinburgh Zoo
Pelusa	10.11.2011	F	Cali	Boa	Edinburgh Zoo
Gabriela	11.11.2011	F	Roca	Boa	Edinburgh Zoo
Valencia	18.11.2011	F	Verde^D	Boa	Edinburgh Zoo
Ciara	18.11.2011	F	Yendi	Boa	Edinburgh Zoo

^{D}=Deceased

Appendix IV. *Data collection sheets*

West group scan

Date:__________ Time:______________ Weather: Clear/Light Clouds/Cloudy/Overcast/Rain/Wind

***Species /Age**	**Name**	**Sex**	**Location**			**Zone**	**Height**				**Behaviour**	**Notes**
			O	**CI**	**SI**		**0**	**1**	**2**	**3**		
C/A	Diego	M										
C/A	Lana	F										
C/A	Santiago	F										
C/A	Sylviana	F										
C/A	Toka	M										
C/A	Figo	M										
C/A	Pedra	F										
C/A	Mekoe	M										
C/A	Inti	M										
C/SA	Rufo	M										
C/SA	Ximo	M										
C/SA	Torres	M										
C/SA	Luna	F										
C/SA	Alba	F										
C/J	Fudge	M										
C/J	Bear	M										
C/J	Hazel	F										
C/J	Pixie	F										
S/A	Hugo	M										
S/A	Gerda	F										
S/A	Jasmin	F										
S/A	Toomi	F										
S/SA	Dita	F										
S/SA	Sancha	F										
S/SA	Orla	F										
S/SA	Gisele	F										
S/J	Loki	F										

*C=*Sapajus* S=*Saimiri* A=Adult SA=Subadult J=juvenile

East group scan

Date:__________ Time:______________ Weather: Clear/Light Clouds/Cloudy/Overcast/Rain/Wind

*Species /Age	Name	Sex	Location			Zone	Height				Behaviour	Notes
			O	CI	SI		0	1	2	3		
C/A	Popeye	M										
C/A	Anita	F										
C/A	Junon	F										
C/A	Kato	M										
C/A	Manuel	M										
C/A	Penelope	F										
C/A	Carlos	M										
C/A	Chico	M										
C/SA	Rosa	F										
C/SA	Ruben	M										
C/SA	Sol	F										
C/SA	Flojo	M										
C/SA	Lindo	F										
C/J	Willow	F										
C/J	Nena	F										
C/J	Gustavo	M										
C/J	Neve	F										
S/A	Boa	M										
S/A	Tatu	F										
S/A	Roca	F										
S/A	Maya	F										
S/A	Elie	F										
S/A	Cali	F										
S/A	Pica	F										
S/A	Yendi	F										
S/A	Flora	F										
S/A	Sipi	F										
S/SA	Lexi	F										
S/SA	Dora	F										
S/SA	Amarilla	F										
S/SA	Pelusa	F										
S/SA	Gabriela	F										
S/SA	Valencia	F										
S/SA	Ciara	F										

*C=*Sapajus* S=*Saimiri* A=Adult SA=Subadult J=juvenile

West *Sapajus* focal

Date:__________ **Time:**_________ **Weather:** Clear/Light Clouds/Cloudy/Overcast/ Rain/Wind **Temp:**________ **Focal:**_________

Interval	**Location**	**Diego**	**Lana**	**Santi**	**Sylvie**	**Pedra**	**Toka**	**Figo**	**Mekoe**	**Inti**	**Rufo**	**Ximo**	**Torres**	**Luna**	**Alba**	**Fudge**	**Bear**	**Hazel**	**Pixie**	***Saimiri***
1	In / Out																			
2	In / Out																			
3	In / Out																			
4	In / Out																			
5	In / Out																			
6	In / Out																			
7	In / Out																			
8	In / Out																			
9	In / Out																			
10	In / Out																			

F = Feed/Forage
FS = Food share
FB = Food beg
FT = Food steal
A/a = Aggression
C = Coalition/support
G/g = Allogroom
L = Locomotion
P = Play
AL = Alert
V = Vigilant
R = Rest (including sleeping)

West *Saimiri* focal

Date:__________ **Time:**_________ **Weather:** **Clear/Light Clouds/Cloudy/Overcast/ Rain/Wind** **Temp:**________ **Focal:**_________

Interval	Location	Hugo	Gerda	Jasmin	Toomi	Dita	Sancha	Orla	Gisele	Loki	*Sapajus*
1	In / Out										
2	In / Out										
3	In / Out										
4	In / Out										
5	In / Out										
6	In / Out										
7	In / Out										
8	In / Out										
9	In / Out										
10	In / Out										

F = Feed/Forage
FS = Food share
FB = Food beg
FT = Food steal
A/a = Aggression
C = Coalition/support
G/g = Allogroom
L = Locomotion
P = Play
AL = Alert
V = Vigilant
R = Rest (including sleeping)

East *Sapajus* focal

Date:__________ **Time:**_________ **Weather:** **Clear/Light Clouds/Cloudy/Overcast/ Rain/Wind** **Temp:**________ **Focal:**_________

Interval	**Location**	**Popeye**	**Manuel**	**Kato**	**Anita**	**Peny**	**Junon**	**Carlos**	**Chico**	**Rosa**	**Ruben**	**Sol**	**Flojo**	**Lindo**	**Willow**	**Nena**	**Gus**	**Neve**	***Saimiri***
1	In / Out																		
2	In / Out																		
3	In / Out																		
4	In / Out																		
5	In / Out																		
6	In / Out																		
7	In / Out																		
8	In / Out																		
9	In / Out																		
10	In / Out																		

F = Feed/Forage **FS** = Food share **FB** = Food beg **FT** = Food steal **A/a** = Aggression **C** = Coalition/support
G/g = Allogroom **L** = Locomotion **P** = Play **AL** = Alert **V** = Vigilant **R** = Rest (including sleeping)

East *Saimiri* focal

Date:__________ **Time:**_________ **Weather:** Clear/Light Clouds/Cloudy/Overcast/ Rain/Wind **Temp:**________ **Focal:**_________

Interval	Location	Boa	Tatu	Roca	Maya	Elie	Cali	Pica	Yendi	Flora	Sipi	Lexi	Dora	Amarilla	Pelusa	Gabriela	Valencia	Ciara	*Sapajus*
1	In / Out																		
2	In / Out																		
3	In / Out																		
4	In / Out																		
5	In / Out																		
6	In / Out																		
7	In / Out																		
8	In / Out																		
9	In / Out																		
10	In / Out																		

F = Feed/Forage
G/g = Allogroom
FS = Food share
L = Locomotion
FB = Food beg
P = Play
FT = Food steal
AL = Alert
A/a = Aggression
V = Vigilant
C = Coalition/support
R = Rest (including sleeping)

Appendix V. *Ethical Approval for studies at the Living Links to Human Evolution Research Centre, RZSS, Edinburgh Zoo*

PSYCHOLOGY DIVISION ETHICAL APPROVAL FORM

Check one box: ☐ STAFF project ☐ UNDERGRADUATE project ☒ POSTGRADUATE project

Title of project Mixed communities of capuchin (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) – A social network approach.

Name of Researcher(s) Sophia Daoudi (Principle Investigator); Gal Badihi (Research Assistant, University of St Andrews)

Email Address s.m.daoudi1@stir.ac.uk

Name of Supervisor(s) (for student research) Prof. Hannah Buchanan-Smith

Date 13/2/15

Postgraduate and Staff Projects

Please indicate your source of funding (Division, Research Council, Govt, Charity, etc)
Self funded

		Yes	No	N/A
1	Will you tell participants that their participation is voluntary?	☐	☐	☒
2	Will you tell participants that they may withdraw at any time and for any reason?	☐	☐	☒
3	Will you obtain written consent for participation?	☐	☐	☒
4	Will you tell participants that their data will be treated with full confidentiality and that, if published, it will not be identifiable as theirs?	☐	☐	☒
5	If an experiment, will you describe the main experimental procedures to participants in advance, so that they are informed about what to expect?	☐	☐	☒
6	With questionnaires, will you give participants the option of omitting any questions they do not want to answer?	☐	☐	☒
7	If the research is observational, will you ask participants for their consent to being observed?	☐	☐	☒
8	Will you debrief participants at the end of their participation (i.e. give them a brief explanation of the study)?	☐	☐	☒

If you have ticked **No** to any of Q1-8, you should normally **tick box B** overleaf; if not, please give an explanation on a separate sheet.. [Note: N/A = not applicable]

			Yes	No	N/A
9	Will your project involve deliberately misleading participants in any way?		☐	☐	☒
10	Is there any realistic risk of you or any participants experiencing either physical or psychological discomfort, distress or harm?		☐	☒	☐
11	Will you be administering drugs or other substances to your participants, or taking fluid or other samples from them?		☐	☒	☐
12	Does your project involve work with animals?		☒	☐	☐
13	Do participants fall into any of the following special groups? If they do please refer to BPS guidelines, and **tick box B** overleaf. Note that you may also need to obtain satisfactory CRB clearance (or equivalent for overseas students)	Schoolchildren (under 18yrs)	☐	☒	☐
		People with learning or communication difficulties	☐	☒	☐
		Patients	☐	☒	☐
		People in custody	☐	☒	☐
		People engaged in illegal activities (e.g. drug taking)	☐	☒	☐

If you have ticked **Yes** to any of Q9 - 13 you should normally **tick box B** overleaf; if not, please give an explanation on a separate sheet.

DECLARATION
I am familiar with the BPS Guidelines for ethical practices in psychological research. I understand that there is an obligation on the lead researcher to bring to the attention of the Ethics Committee any issues with ethical implications not clearly covered by the checklist.

Please tick to confirm: ☒
PLEASE TICK **EITHER** BOX A OR BOX B BELOW AND **PROVIDE THE DETAILS REQUIRED** IN SUPPORT OF YOUR APPLICATION.

	Please tick
B. I consider that this project **may** have ethical implications that should be brought before the Division committee, and/or it will be carried out with children or other vulnerable populations	☒
Please provide details on a separate sheet.	

Checklist for a Part B submission:-	**Please tick**
• Project title	☒
• Purpose of project and its academic rationale	☒
• Number of participants (age, gender, exclusion/inclusion criteria) and how they will be recruited	☒
• Start and end dates	☒
• Brief description of methods and measurements	☒
o Where participants will be tested	☐
o How materials will be administered	☐
o Any novel questions or questionnaires are included with submission	☐
o Length of time for each participant	☐
• Information/ consent form attached	☐
o Participant allowed to withdraw at any time	☐
o All individual data will be confidential	☐
• Debriefing form attached	☐
• A clear but concise statement of ethical considerations raised by the project and how you intend to deal with them.	☒

This form should be submitted by email to the Psychology Ethics Committee for consideration (psychethicssubs@stir.ac.uk). Please include the name of the applicant in the 'Subject' line of the email. Students should send the form to their supervisor who, after checking it, will forward it to the Psychology Ethics Committee.

Project Title

Mixed communities of capuchins (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) – A social network approach

Sophia Daoudi, PhD student supervised by Hannah Buchanan-Smith

Purpose of project and its academic rationale

The proposed research is an observational study of the mixed species exhibit of capuchin (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*), housed in the Scottish Primate Research Group "Living Links to Human Evolution Research Centre", Edinburgh Zoo. These species are known to associate in the wild, forming temporary stable mixed species groups. Previous research on mixed species exhibits involving primates that are sympatric in the wild have shown positive results (Sodaro, 1999; Hardie, Prescott & Buchanan-Smith, 2003; Leonardi et al., 2011). However, previous research (Sodaro, 1999; Dalton & Buchanan-Smith, 2005; Buchanan-Smith et al., 2013) has also highlighted that with ever changing dynamics, mixed species groups need continued careful monitoring, in order to ensure that welfare is not compromised.

The results of the previous studies (Leonardi et al., 2011; Buchanan-Smith et al., 2013) conducted over 3 consecutive years (2008, 2009, 2010) found that in both East and West groups, *Sapajus* and *Saimiri* spent an estimated 80% of their time in shared enclosures, with *Saimiri* observed in the *Sapajus* indoor enclosure across all 3 years. The amount and type of observed interspecific interactions varied between studies, with more affiliative interactions occurring between species after Phase 2 in 2008 (mainly 'curious approach' and play), and less in 2009 and 2010, with *Saimiri* hardly ever observed initiating interactions with *Sapajus*. Although 'curious approach' and 'play' continued to be the most observed affiliative behaviours in the 2009 and 2010 studies, these were initiated more by *Sapajus* and would occasionally be responded to with aggression by *Saimiri*. Though the results indicated an increase in aggressive interspecific interactions (chase contact) this does not necessarily indicate poor welfare, as these behaviours have also been observed in the wild (Terborgh, 1983). Furthermore, in terms of enclosure use and height level occupied, Leonardi et al. (2011) found that the West *Sapajus* occupied heights >4m whereas the East *Sapajus* were more evenly distributed between the different height levels (ground, <2m, 2-4m, >4m) and both *Saimiri* groups were distributed across the vertical dimension.

The data collected in both wild and captive research on *Sapajus* and *Saimiri* thus far represents either the percentage of associations, frequencies of interactions and/or proximities. It is clear that more research is needed in order to gain a better understanding of behaviour in mixed species groups. One way of achieving this, is to apply the use of social network analysis, which should enable us to identify and quantify specific attributes of social relationships at the individual level. This method of analysis has already been applied in captive single groups of *Sapajus* (Dufour et al., 2011; Morton, 2014) and *Saimiri* (Dufour et al., 2011; Claidière et al., 2013) at Living Links, however no previous study has yet examined this in mixed *Sapajus*/*Saimiri* exhibits.

Proposed project

The proposed project will aim to determine the position of individuals within a social network based on spatial proximity and frequency of interactions. Additionally we will be looking to see whether factors such as sex, age and/or hierarchy determine network position.

It is predicted that a network based on affiliative interactions would show juvenile *Sapajus* and *Saimiri* interacting more frequently than adults (Fig 1). However, if aggressive interactions between the two species are still prominent then it will be interesting to determine whether this occurs more frequently between specific dyads.

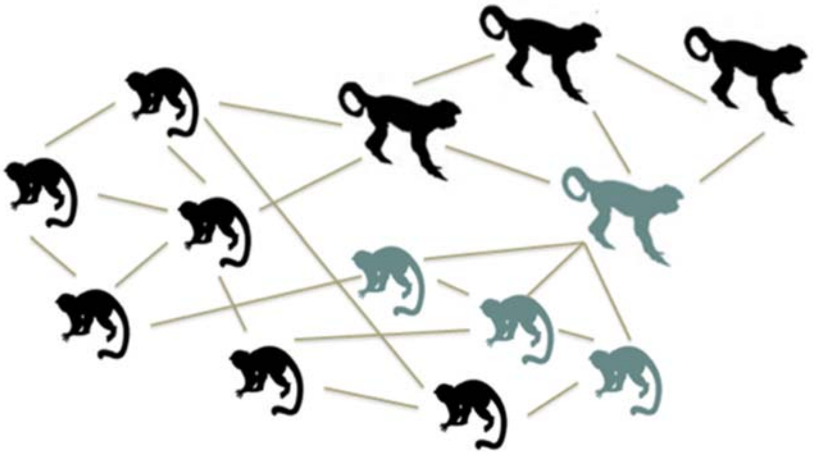

Figure 1. Hypothetical network of *Sapajus*/*Saimiri* mixed groups at Living Links. Images in black indicate adults and images in blue indicate juveniles.

In addition, data will be collected on the use of shared enclosures by both species (i.e. the outdoor enclosure and capuchin indoor enclosure). A grid will be used to determine the location, behaviour and height level of individuals.

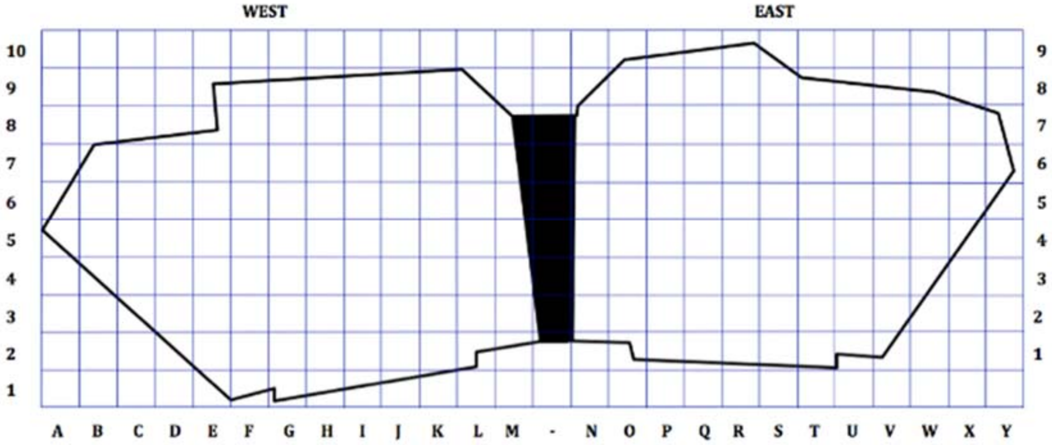

Figure 2. Example grid of the Living Links West and East outdoor enclosures.

Brief description of methods and measurements

Study animals, housing and husbandry. Two mixed species groups of *Sapajus* and *Saimiri* at Living Links.

Data collection. PI – Focal sampling will be used to collect data on each (reliably identifiable) individual for a period of 10 min; behaviours such as activity and proximity will be recorded in 1 min intervals using point sampling (Martin & Bateson, 2007), together with all occurrences of interactions. Data will be recorded onto datasheets, or hand-held computer to record the focal's location and activities (e.g. locomote, forage, allogroom, resting, etc.) and the proximity of the nearest neighbour. Any interspecific interactions observed will be recorded *ad libitum*.

RA – Scan sampling will be used to collect the enclosure use data (Martin & Bateson, 2007); the species (*Sapajus* = C and *Saimiri* = S), location, behaviour (as above) and height level (ground level, ≤2m, 2-4m, ≥4m) will be recorded onto datasheets (e.g. Figure 2).

The study would be conducted in collaboration with Dr. Blake Morton and the dedicated team at Living Links as part of the ongoing "Living Together" project (under Prof. Buchanan-Smith's direction).

References cited

Buchanan-Smith, H.M., Griciute, J., Daoudi, S., Leonardi, R., & Whiten, A. (2013). Interspecific interactions and welfare implications in mixed species communities of capuchin (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) over 3 years. *Applied Animal Behaviour Science* 147:324-333.

Claidière, N., Messer, E.J.E., Hoppitt, W., & Whiten, A. (2013). Diffusion Dynamics of Socially Learned Foraging Techniques in Squirrel Monkeys. *Current Biology* 23:1251-1255.

Dalton, R. & Buchanan-Smith, H.M. (2005). A Mixed Species Exhibit for Goeldi's monkeys and Pygmy Marmosets at Edinburgh Zoo. *International Zoo Yearbook*, 39: 176-184.

Dufour V., Sueur C., Whiten A., & Buchanan-Smith H.M. (2011). The Impact of Moving to a Novel Environment on Social Networks, Activity and Wellbeing in Two New World Primates. *American Journal of Primatology* 78:802-811.

Hardie S.M., Prescott M.J. & Buchanan-Smith H.M. (2003). Ten years of tamarin mixed-species troops at Belfast zoological gardens. *Primate Report* 65:21–38.

Leonardi, R., Buchanan-Smith, H.M., Dufour, V., MacDonald, C., & Whiten, A. (2011). Living together: Behaviour and welfare in single and mixed species groups of capuchin (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology*, 72:33-47.

Martin, P., & Bateson, P. P. G. (1993). *Measuring behaviour: an introductory guide*. Cambridge University Press.

Morton, F.B. (2014). Individual Differences in Learning, Personality, and Social Success in Brown Capuchin Monkeys (*Sapajus apella*). *Unpublished doctoral thesis, University of Stirling*, p295.

Sodaro V. (1999). Housing and exhibition of mixed species of neotropical primates. Brookfield: Chicago Zoological Society.Terborgh, J. (1983). Five New World Primates: A Study in Comparative Ecology. *Princeton University Press.* 260p.

RE: Sophia Daoudi ethics
Psychology Ethics Submissions

Fri 13/02/2015 10:41
To:
Sophia Daoudi;
Cc:
Psychology Ethics Submissions;
Hannah Buchanan-Smith;
You forwarded this message on 03/03/2015 15:56.

Dear Sophia,
Your project titled:
“Mixed communities of capuchin (Sapajus apella) and squirrel monkeys (Saimiri sciureus) – A social network approach”
has been approved by the Psychology Ethics Committee.
Regards,
Lindsay

Lindsay Wilson
Chair, Psychology Ethics Committee

From: Hannah Buchanan-Smith
Sent: 13 February 2015 09:17
To: Psychology Ethics Submissions
Cc: Sophia Daoudi
Subject: Sophia Daoudi ethics

Please find attached an ethics submission for Sophia Daoudi –this is a purely observational study and I see no ethical concerns.

Best, Hannah

Check out: New methods for monitoring and improving welfare of laboratory dogs

Hannah M. Buchanan-Smith
Professor, Behaviour and Evolution Research Group
Director of Learning and Teaching in SNS

Psychology, School of Natural Sciences
University of Stirling
Stirling, FK9 4LA
Scotland
Tel: 01786 467674
Fax: 01786 467641
E-mail: h.m.buchanan-smith@stir.ac.uk
Home page: https://rms.stir.ac.uk/converis-stirling/person/11925
http://marmosetcare.com/

Appendix VI. *Coefficients of relatedness in the Living Links monkeys*

Table 9.5 *Estimated relatedness of the West* Sapajus *group.*

	Diego	Lana	Santi	Sylvie	Toka	Figo	Pedra	Mekoe	Inti	Rufo	Ximo	Torres	Luna	Alba	Fudge	Bear	Hazel	Pixie	**Coeff. of relatedness**
Diego		0	0	0	0	0	0	0	0.25	0.25	0.25	0.25	0.5	0.5	0.5	0.5	0.5	0.5	**0.235294**
Lana	0		0.5	0.5	0.5	0.5	0.5	0.25	0.25	0.5	0.25	0.25	0.5	0.25	0.5	0.25	0.25	0.25	**0.352941**
Santiago	0	0.5		0.5	0.5	0.5	0.5	0.375	0.25	0.25	0.5	0.25	0.25	0.5	0.25	0.5	0.25	0.25	**0.360294**
Sylvania	0	0.5	0.5		0.5	0.5	0.5	0.5	0.5	0.25	0.25	0.5	0.25	0.25	0.25	0.25	0.5	0.25	**0.367647**
Toka	0	0.5	0.5	0.5		0.5	0.5	0.375	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	**0.316176**
Figo	0	0.5	0.5	0.5	0.5		0.5	0.375	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	**0.316176**
Pedra	0	0.5	0.5	0.5	0.5	0.5		0.375	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.5	**0.330882**
Mekoe	0	0.25	0.375	0.5	0.375	0.375	0.375		0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	**0.279412**
Inti	0.25	0.25	0.25	0.5	0.25	0.25	0.25	0.25		0.25	0.25	0.5	0.125	0.125	0.125	0.125	0.25	0.125	**0.242647**
Rufo	0.25	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.25		0.25	0.25	0.5	0.25	0.125	0.25	0.25	0.25	**0.272059**
Ximo	0.25	0.25	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.25		0.25	0.25	0.25	0.25	0.25	0.125	0.125	**0.25**
Torres	0.25	0.25	0.25	0.5	0.25	0.25	0.25	0.25	0.5	0.25	0.25		0.25	0.25	0.25	0.125	0.25	0.125	**0.264706**
Luna	0.5	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.125	0.5	0.25	0.25		0.25	0.25	0.25	0.25	0.25	**0.286765**
Alba	0.5	0.25	0.5	0.25	0.25	0.25	0.25	0.25	0.125	0.25	0.25	0.25	0.25		0.25	0.25	0.125	0.125	**0.257353**
Mr Fudge	0.5	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.125	0.125	0.25	0.25	0.25	0.25		0.25	0.25	0.25	**0.264706**
Bear	0.5	0.25	0.5	0.25	0.25	0.25	0.25	0.25	0.125	0.25	0.25	0.125	0.25	0.125	0.25		0.25	0.25	**0.257353**
Hazel	0.5	0.25	0.25	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.125	0.25	0.25	0.125	0.25	0.25		0.25	**0.264706**
Pixie	0.5	0.25	0.25	0.25	0.25	0.25	0.5	0.25	0.125	0.25	0.125	0.125	0.25	0.125	0.25	0.25	0.25		**0.25**

Table 9.6 *Estimated relatedness of the East* Sapajus *group.*

	Popeye	Anita	Junon	Kato	Manuel	Penelope	Carlos	Chico	Rosa	Reuben	Sol	Flojo	Lindo	Willow	Nena	Gus	Agnes	**Coeff. of relatedness**
Popeye		0	0.5	0	0	0	0.375	0.375	0	0.375	0.5	0.5	0.5	0.5	0.5	0.5	0.5	**0.320313**
Anita	0		0	0	0.5	0.5	0	0	0.5	0	0.25	0.5	0.25	0.5	0.25	0.25	0.5	**0.25**
Junon	0.5	0		0	0	0	0.5	0.5	0	0.5	0	0	0	0	0	0	0	**0.125**
Kato	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Manuel	0	0.5	0	0		0.5	0	0	0.25	0	0.25	0.25	0.25	0.25	0.25	0.25	0.25	**0.1875**
Penelope	0	0.5	0	0	0.5		0	0	0.25	0	0.5	0.25	0.5	0.25	0.5	0.5	0.25	**0.25**
Carlos	0.375	0	0.5	0	0	0		0.5	0	0.5	0	0	0	0	0	0	0	**0.117188**
Chico	0.375	0	0.5	0	0	0	0.5		0	0.5	0	0	0	0	0	0	0	**0.117188**
Rosa	0	0.5	0	0	0.25	0.25	0	0		0.25	0.25	0.5	0.25	0.5	0.25	0.25	0.5	**0.234375**
Reuben	0.375	0	0.5	0	0	0	0.5	0.5	0.25		0.25	0.25	0.25	0.25	0.25	0.25	0.25	**0.242188**
Sol	0.5	0.25	0	0	0.25	0.5	0	0	0.5	0.25		0.5	0.25	0.25	0.5	0.5	0.25	**0.28125**
Flojo	0.5	0.5	0	0	0.25	0.25	0	0	0.5	0.25	0.25		0.25	0.5	0.25	0.25	0.5	**0.265625**
Lindo	0.5	0.25	0	0	0.25	0.5	0	0	0.25	0.25	0.5	0.25		0.25	0.5	0.5	0.25	**0.265625**
Willow	0.5	0.5	0	0	0.25	0.25	0	0	0.5	0.25	0.25	0.5	0.25		0.25	0.25	0.5	**0.265625**
Nena	0.5	0.25	0	0	0.25	0.5	0	0	0.25	0.25	0.5	0.25	0.5	0.25		0.5	0.25	**0.265625**
Gustavo	0.5	0.25	0	0	0.25	0.5	0	0	0.25	0.25	0.5	0.25	0.5	0.25	0.5		0.25	**0.265625**
Agnes	0.5	0.5	0	0	0.25	0.25	0	0	0.5	0.25	0.25	0.5	0.25	0.5	0.25	0.25		**0.265625**

Table 9.7 *Estimated relatedness of the West* Saimiri *group.*

	Hugo	Gerda	Jasmin	Toomi	Dita	Sancha	Orla	Gisele	Loki	**Coeff. of relatedness**
Hugo		0	0	0	0	0	0	0	0.5	**0.0625**
Gerda	0		0.25	0.25	0.5	0.25	0.5	0.5	0.25	**0.3125**
Jasmin	0	0.25		0.5	0.25	0.5	0.25	0.25	0.5	**0.3125**
Toomi	0	0.25	0.5		0.25	0.5	0.25	0.25	0.25	**0.28125**
Dita	0	0.5	0.25	0.25		0.25	0.5	0.5	0.125	**0.296875**
Sancha	0	0.25	0.5	0.5	0.25		0.25	0.25	0.25	**0.28125**
Orla	0	0.5	0.25	0.25	0.5	0.25		0.5	0.125	**0.296875**
Gisele	0	0.5	0.25	0.25	0.5	0.25	0.5		0.125	**0.296875**
Loki	0.5	0.25	0.5	0.25	0.125	0.25	0.125	0.125		**0.265625**

Table 9.8 *Estimated relatedness of the East* Saimiri *group.*

	Boa	Tatu	Roca	Maya	Elie	Cali	Pica	Yendi	Flora	Sipi	Lexi	Dora	Amarilla	Pelusa	Gabriela	Valencia	Ciara	**Coeff. of relatedness**
Boa		0	0	0	0	0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	**0.34375**
Tatu	0		0.25	0.25	0.25	0.25	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	**0.148438**
Roca	0	0.25		0.25	0.25	0.25	0.5	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.5	0.125	0.125	**0.195313**
Maya	0	0.25	0.25		0.25	0.25	0.125	0.5	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.25	**0.179688**
Elie	0	0.25	0.25	0.25		0.25	0.125	0.125	0.5	0.125	0.5	0.125	0.5	0.125	0.125	0.125	0.125	**0.21875**
Cali	0	0.25	0.25	0.25	0.25		0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.5	0.125	0.125	0.125	**0.171875**
Pica	0	0.125	0.5	0.125	0.125	0.125		0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.5	0.25	0.25	**0.234375**
Yendi	0.5	0.125	0.125	0.5	0.125	0.125	0.25		0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.5	**0.265625**
Flora	0.5	0.125	0.125	0.125	0.5	0.125	0.25	0.25		0.25	0.5	0.25	0.5	0.25	0.25	0.25	0.25	**0.28125**
Sipi	0.5	0.125	0.125	0.125	0.125	0.125	0.25	0.25	0.25		0.25	0.5	0.25	0.25	0.25	0.5	0.25	**0.257813**
Lexi	0.5	0.125	0.125	0.125	0.5	0.125	0.25	0.25	0.5	0.25		0.25	0.5	0.25	0.25	0.25	0.25	**0.28125**
Dora	0.5	0.125	0.125	0.125	0.125	0.125	0.25	0.25	0.25	0.5	0.25		0.25	0.25	0.25	0.5	0.25	**0.257813**
Amarilla	0.5	0.125	0.125	0.125	0.5	0.125	0.25	0.25	0.5	0.25	0.5	0.25		0.25	0.25	0.25	0.25	**0.28125**
Pelusa	0.5	0.125	0.125	0.125	0.125	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.25		0.25	0.25	0.25	**0.25**
Gabriela	0.5	0.125	0.5	0.125	0.125	0.125	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.25		0.25	0.25	**0.265625**
Valencia	0.5	0.125	0.125	0.125	0.125	0.125	0.25	0.25	0.25	0.5	0.25	0.5	0.25	0.25	0.25		0.25	**0.257813**
Ciara	0.5	0.125	0.125	0.25	0.125	0.125	0.25	0.5	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25		**0.25**

Appendix VII. *Social network Analyses (SNAs)*

Table 9.9 *Mixed-species SNAs for the West* Sapajus *(n=18) and* Saimiri *(n=9) groups.*

Name	**ID (node)**	**Sex**	**Age**	**Strength**	**Eigenvector Centrality**	**Reach**	**Clustering Coefficient**	**Affinity**
Diego	1	M	12.5	693	0.33	523155	0.44	754.91
Lana	2	F	19.0	850	0.41	649183	0.44	763.74
Santiago	3	F	13.0	787	0.38	597618	0.44	759.36
Sylvania	4	F	11.5	289	0.07	141734	0.12	490.43
Toka	5	M	10.0	388	0.1	196102	0.15	505.42
Figo	6	M	9.0	293	0.08	159226	0.17	543.43
Pedra	7	F	7.0	338	0.09	174696	0.15	516.85
Mekoe	8	M	7.0	292	0.04	112949	0.11	386.81
Inti	9	M	5.0	204	0.04	95049	0.11	465.93
Rufo	10	M	5.0	300	0.05	120993	0.11	403.31
Ximo	11	M	5.0	383	0.1	199702	0.15	521.42
Torres	12	M	4.0	381	0.06	157923	0.11	414.5
Luna	13	F	4.0	272	0.05	124629	0.13	458.19
Alba	14	F	3.0	334	0.05	132681	0.1	397.25
Mr Fudge	15	M	1.5	942	0.42	683094	0.36	725.15
Bear	16	M	1.5	929	0.39	640823	0.32	689.8
Hazel	17	F	1.0	555	0.23	374102	0.31	674.06
Pixie	18	F	1.0	823	0.38	611842	0.4	743.43
Hugo	19	M	4.5	94	0	49276	0.35	524.21
Gerda	20	F	15.0	680	0	383383	0.36	563.8
Jasmin	21	F	12.0	643	0	370606	0.38	576.37
Toomi	22	F	8.0	560	0	312765	0.37	558.51
Dita	23	F	5.0	592	0	327351	0.37	552.96
Sancha	24	F	5.0	491	0	261128	0.33	531.83
Orla	25	F	3.0	442	0	247227	0.37	559.34
Gisele	26	F	2.5	546	0	305516	0.38	559.55
Loki	27	F	1.0	473	0	240591	0.28	508.65

Table 9.10 *Mixed-species SNAs for the East* Sapajus *(n=17) and* Saimiri *(n=17) groups.*

Name	**ID (node)**	**Sex**	**Age**	**Strength**	**Eigenvector Centrality**	**Reach**	**Clustering Coefficient**	**Affinity**
Popeye	1	M	13.5	215.07	0.3	348248	0.38	599.39
Anita	2	F	17.0	219.34	0.29	339908	0.35	574.17
Junon*	3	F	14.5	72.98	0.02	65745	0.2	335.43
Kato*	4	M	9.5	30.55	0.02	33614	0.14	409.93
Manuel	5	M	11.0	151.65	0.21	244982	0.38	597.52
Penelope	6	F	9.0	238.63	0.33	384102	0.38	596.43
Carlos*	7	M	8.5	69.14	0.03	62242	0.24	334.63
Chico*	8	M	6.0	79.84	0.03	73889	0.16	345.28
Rosa	9	F	5.0	83.91	0.08	108359	0.17	479.46
Ruben*	10	M	4.5	141.13	0.06	120240	0.1	316.42
Sol	11	F	4.5	132.76	0.15	189552	0.25	530.96
Flojo	12	M	3.5	271.39	0.36	427843	0.34	582.89
Lindo	13	F	3.5	194.78	0.28	324616	0.4	618.32
Willow	14	F	2.0	128.66	0.16	196164	0.31	568.59
Nena	15	F	2.0	222.69	0.31	370572	0.4	617.62
Gustavo	16	M	1.0	310.25	0.42	482926	0.34	576.28
Agnes	17	F	1.0	251.76	0.35	403075	0.37	592.76
Boa	18	M	9.0	101.47	0.02	115400	0.18	422.71
Tatu	19	F	14.0	143.84	0.02	165078	0.22	426.56
Roca	20	F	12.0	120.55	0.01	117255	0.14	360.78
Maya	21	F	11.0	60.35	0.01	55371	0.14	341.8
Elie	22	F	9.0	204.7	0.03	269183	0.33	487.65
Cali	23	F	9.0	177.21	0.03	190279	0.2	398.91
Pica	24	F	7.0	71.08	0.01	67106	0.14	351.34
Yendi	25	F	6.0	98.39	0.02	89754	0.1	339.98
Flora	26	F	6.0	211.06	0.04	278136	0.33	487.96
Sipi	27	F	5.0	142.84	0.02	162386	0.25	421.78
Lexi	28	F	4.0	229.18	0.04	298160	0.31	482.46
Dora	29	F	4.0	138.23	0.03	174895	0.27	468.89
Amarilla	30	F	3.0	216.15	0.04	288852	0.34	494.61
Pelusa	31	F	3.0	167.51	0.02	182948	0.2	405.65
Gabriela	32	F	3.0	115.79	0.01	111742	0.13	359.3
Valencia	33	F	3.0	94.1	0.02	97733	0.13	386.3
Ciara	34	F	3.0	109.53	0.02	117391	0.15	399.29

Table 9.11 *Single-species SNAs for the West* Sapajus *(n=18).*

Name	ID (node)	Sex	Age	Strength	Eigenvector Centrality	Reach	Clustering Coefficient	Affinity
Diego	1	M	12.5	693	0.33	522496	0.46	753.96
Lana	2	F	19.0	850	0.41	648399	0.46	762.82
Santiago	3	F	13.0	786	0.38	596419	0.46	758.8
Sylvania	4	F	11.5	286	0.07	139204	0.13	486.73
Toka	5	M	10.0	388	0.1	194864	0.15	502.23
Figo	6	M	9.0	292	0.08	158074	0.18	541.35
Pedra	7	F	7.0	330	0.09	169667	0.16	514.14
Mekoe	8	M	7.0	289	0.04	110016	0.12	380.68
Inti	9	M	5.0	190	0.04	86927	0.14	457.51
Rufo	10	M	5.0	296	0.05	117792	0.12	397.95
Ximo	11	M	5.0	383	0.1	198174	0.16	517.43
Torres	12	M	4.0	372	0.06	152586	0.12	410.18
Luna	13	F	4.0	269	0.05	122064	0.14	453.77
Alba	14	F	3.0	326	0.05	127754	0.11	391.88
Mr Fudge	15	M	1.5	942	0.42	681770	0.38	723.75
Bear	16	M	1.5	927	0.39	638543	0.34	688.83
Hazel	17	F	1.0	555	0.23	373299	0.33	672.61
Pixie	18	F	1.0	822	0.38	610350	0.43	742.52

Table 9.12 *Single-species SNAs for the West* Saimiri *(n=9) groups.*

Name	ID (node)	Sex	Age	Strength	Eigenvector Centrality	Reach	Clustering Coefficient	Affinity
Hugo	19	M	4.5	94	0.05	48352	0.35	514.38
Gerda	20	F	15.0	679	0.44	378753	0.37	557.81
Jasmin	21	F	12.0	636	0.42	364712	0.39	573.45
Toomi	22	F	8.0	550	0.35	306002	0.38	556.37
Dita	23	F	5.0	589	0.37	322735	0.38	547.94
Sancha	24	F	5.0	483	0.29	254492	0.34	526.9
Orla	25	F	3.0	434	0.28	241435	0.38	556.3
Gisele	26	F	2.5	545	0.35	300984	0.38	552.26
Loki	27	F	1.0	454	0.27	231115	0.31	509.06

Table 9.13 *Single-species SNAs for the East* Sapajus *(n=17).*

Name	**ID (node)**	**Sex**	**Age**	**Strength**	**Eigenvector Centrality**	**Reach**	**Clustering Coefficient**	**Affinity**
Popeye	1	M	13.5	568	0.3	331677	0.4	583.94
Anita	2	F	17.0	578	0.3	323105	0.37	559.01
Junon*	3	F	14.5	160	0.02	46276	0.31	289.23
Kato*	4	M	9.5	69	0.02	27405	0.19	397.17
Manuel	5	M	11.0	395	0.21	232522	0.41	588.66
Penelope	6	F	9.0	627	0.33	366395	0.4	584.36
Carlos*	7	M	8.5	176	0.03	52615	0.28	298.95
Chico*	8	M	6.0	193	0.03	60713	0.2	314.58
Rosa	9	F	5.0	197	0.08	92166	0.22	467.85
Ruben*	10	M	4.5	340	0.06	96637	0.12	284.23
Sol	11	F	4.5	325	0.15	170084	0.3	523.34
Flojo	12	M	3.5	715	0.37	406408	0.36	568.4
Lindo	13	F	3.5	513	0.28	308583	0.42	601.53
Willow	14	F	2.0	319	0.16	178883	0.37	560.76
Nena	15	F	2.0	573	0.32	348723	0.44	608.59
Gustavo	16	M	1.0	823	0.42	460283	0.35	559.27
Agnes	17	F	1.0	661	0.35	380741	0.39	576.01

Table 9.14 *Single-species SNAs for the East* Saimiri *(n=17).*

Name	**ID (node)**	**Sex**	**Age**	**Strength**	**Eigenvector Centrality**	**Reach**	**Clustering Coefficient**	**Affinity**
Boa	18	M	9.0	237	0.15	96677	0.24	407.92
Tatu	19	F	14.0	359	0.18	144316	0.27	401.99
Roca	20	F	12.0	318	0.14	108092	0.15	339.91
Maya	21	F	11.0	161	0.06	51811	0.15	321.81
Elie	22	F	9.0	539	0.4	248918	0.37	461.81
Cali	23	F	9.0	450	0.21	168068	0.24	373.48
Pica	24	F	7.0	190	0.08	62722	0.15	330.12
Yendi	25	F	6.0	227	0.09	70830	0.13	312.03
Flora	26	F	6.0	530	0.4	248279	0.4	468.45
Sipi	27	F	5.0	365	0.17	144559	0.3	396.05
Lexi	28	F	4.0	583	0.43	269015	0.38	461.43
Dora	29	F	4.0	346	0.24	154397	0.33	446.23
Amarilla	30	F	3.0	565	0.43	263800	0.39	466.9
Pelusa	31	F	3.0	421	0.2	162163	0.25	385.19
Gabriela	32	F	3.0	295	0.13	99713	0.15	338.01
Valencia	33	F	3.0	224	0.11	80569	0.17	359.68
Ciara	34	F	3.0	270	0.14	99113	0.18	367.09

Appendix VIII. *Recommendations for planned refurbishment at Living Links*

Proposal for Living Links Outdoor Enclosure Refurbishment

Meeting Thursday 20th July 2017
Donald Gow (Team Leader for Living Links and the Budongo Trail)
Professor Hannah M. Buchanan-Smith (University of Stirling), and
Sophia Daoudi (PhD student, University of Stirling and Living Links Researcher)

The outdoor enclosures at Living Links are well designed to allow the monkeys to express a range of natural behaviours. However overtime (partly due to the destructive nature of the capuchins) the large trees occupying the central areas have lost most of their horizontal branches, foliage, and it has also been confirmed that they are potentially unstable (a potential health and safety risk).

Based on a combination of research undertaken at Living Links from June-August 2015 (for more details see Daoudi, Badihi & Buchanan-Smith, 2017), and research in the wild at Raleighvallen Nature Reserve, Suriname, we offer suggestions for refurbishment to the enclosures. The overall goals are to encourage: better use of space (both vertically and horizontally); more natural behaviours in terms of activity time budgets and species-typical locomotion; and more affiliative and fewer aggressive behaviours (inter- & intra-specifically).

Living Links

Both East and West *Sapajus* groups spend a good proportion of time outdoors with the East more often than the West (Appendix I, Table 1; 80% vs. 49% of 90 scans respectively). Both *Sapajus* groups show a preference for the central tall tree areas of their outdoor enclosures, with the East group observed in central zone 6 for 48% of scans, and the West group in central zone 8 for 36% of scans (Appendix I, Fig. 1). Peripheral zones were utilized less than expected.

In contrast both *Saimiri* groups spent less time outside (East, 27%; West, 11%) and of this small percentage spent most of their time in the zones in close proximity to the indoor enclosure entrances (West, 60%, East, 58%, Appendix I, Fig. 1; Table 1). For both *Saimiri* groups the central tree areas were utilized less than expected.

The vertical distribution of East and West *Sapajus* and *Saimiri* groups outdoors is relatively similar, with both species spending most time at levels <2m and on the ground (Appendix i, Fig. 2).

Raleighvallen Nature Reserve

In the wild *Sapajus* and *Saimiri* were generally observed in different sections of the canopy. *Sapajus* were found mostly in the lower and middle levels of the canopy (Appendix ii, Fig. 3). Whereas *Saimiri* were predominantly sighted in the understory and lower levels of the main canopy (Appendix II, Fig. 3), though when *Sapajus* were also present *Saimiri* were observed at higher levels of the canopy. Both species were observed jumping and leaping between trees, and making use of vines and lianas. In addition to this, *Sapajus* would often be observed in and around bamboo patches.

Suggestions for change

1. Remove potentially unsafe verticals and replace with more permanent, solid, but equally high verticals, with notches to allow relaxed sitting for (groups of) monkeys, and to ease connections for horizontals.
2. Bigger, and more horizontal branches, and high up.
3. Breakable branches to allow destruction (e.g. branch shaking, part of natural behavioural repertoire). Holes in the poles to allow insertion of fresh browse might be good.
4. Keep some verticals unconnected to encourage leaps between them.

5. Use of vines and ropes to connect between verticals and to connect *Saimiri* between indoor-outdoor enclosures (especially important for *Saimiri*).
6. Elder bushes placed near West *Saimiri* exit, to encourage use of outdoor enclosure.
7. Elder bushes/other shrubbery near central location to encourage better enclosure use by *Saimiri.*
8. Increase bamboo patches.
9. Wind breaks outside, as this is a limiting factor to outdoor use in winter (unpublished data from Stirling practicals).

Data collection Sophia has agreed to collect data before and after the refurbishment, which would provide an important evidence base of whether the changes have had the desired effect.

Appendix i

Table 1. *The Percentage of Scans (n = 90) Spent in Enclosures, Out of Sight, and Co-present for Both East and West Groups*

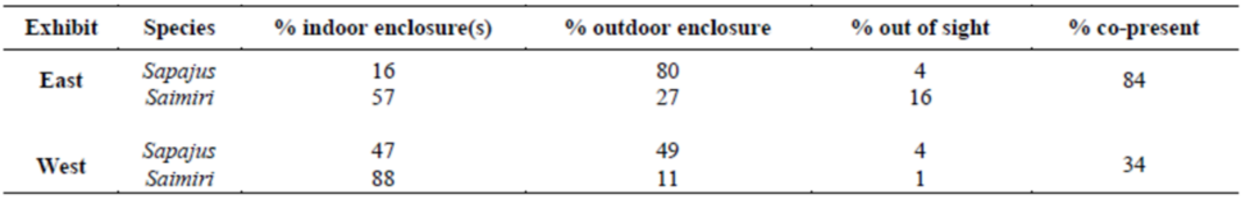

Exhibit	Species	% indoor enclosure(s)	% outdoor enclosure	% out of sight	% co-present
East	*Sapajus*	16	80	4	84
	Saimiri	57	27	16	
West	*Sapajus*	47	49	4	34
	Saimiri	88	11	1	

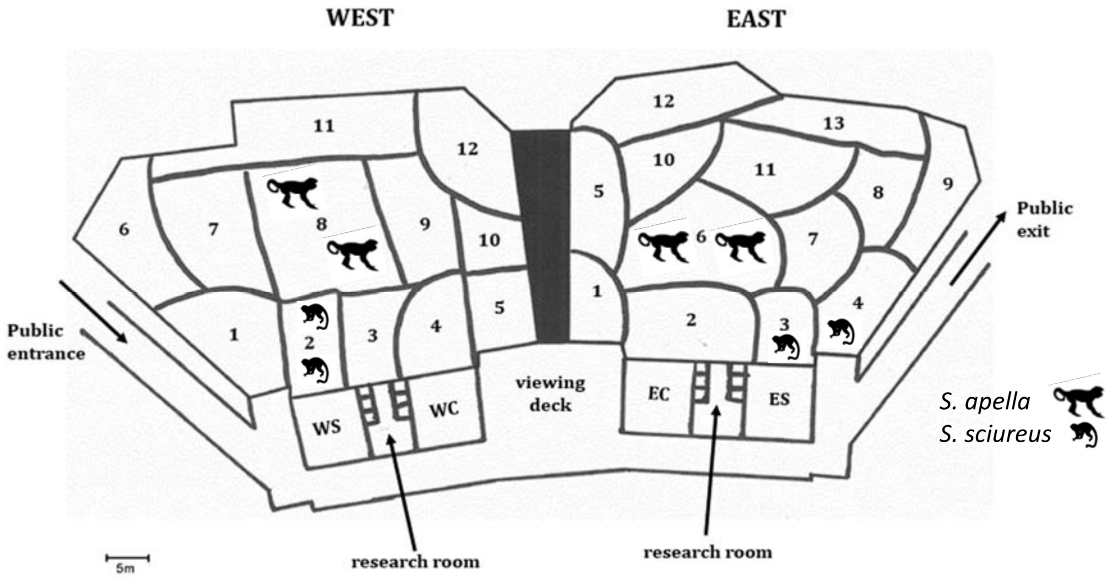

Figure 1. Schematic diagram of the Living Links to Human Evolution Research Centre outdoor enclosures, divided into “meaningful zones” (approximately to scale), for example zone 2 East represents woodchip and tree logs on the ground and zone 3 West represents tall grass and wildflowers (see Daoudi et al. (2017) for details of zones). Key for indoor enclosures: WS and WC = West squirrel monkeys and West capuchins; ES and EC = East squirrel monkeys and East capuchins.

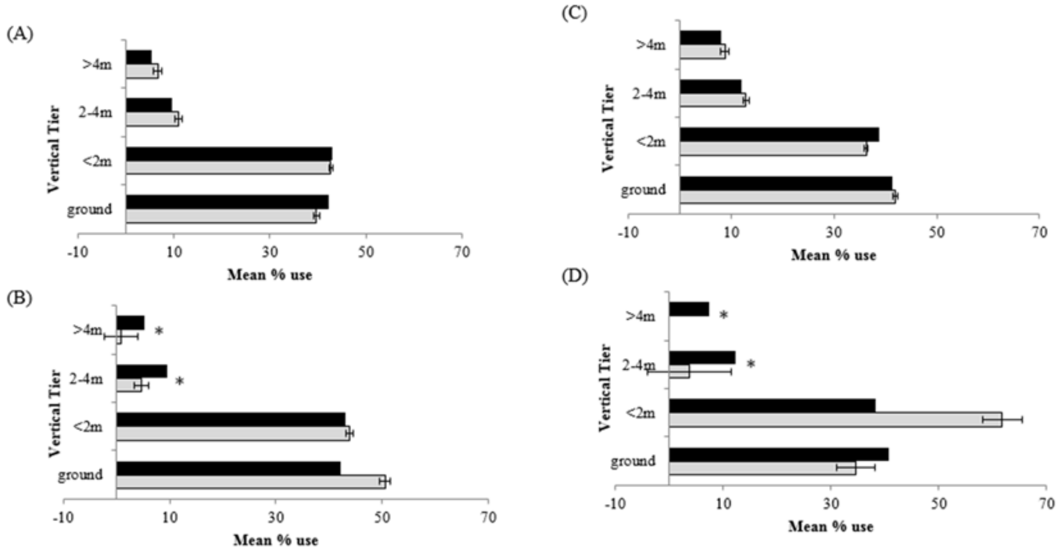

Figure 2. Use of four vertical tiers in the East and West outdoor enclosures (*n* = 90) including ± S.E bars for **A)** East *Sapajus,* **B)** East *Saimiri*, **C)** West *Sapajus* and **D)** West *Saimiri*. An asterisk (*) indicates a significant difference between observed (light bars) and expected (dark bars) values.

Appendix ii

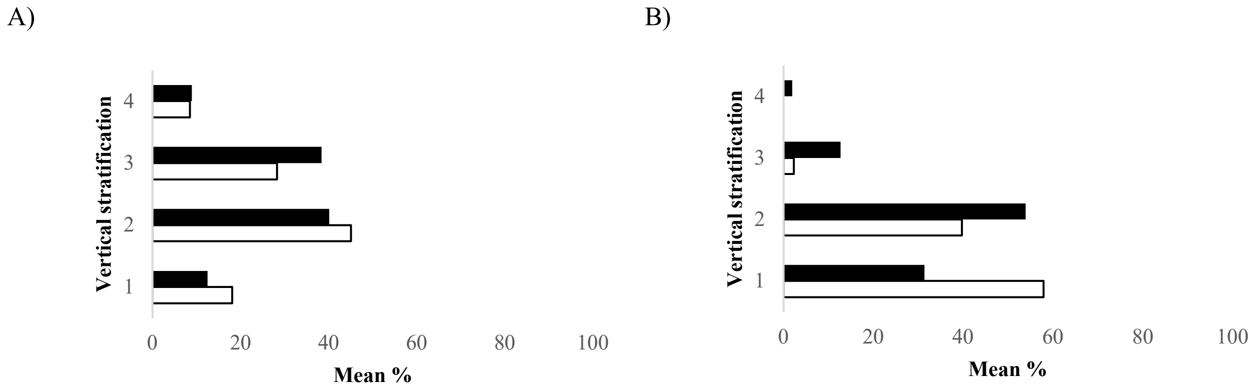

Figure 2. Use of forest strata based on troop sightings of (A) *Sapajus apella* (*n*=54) and (B) *Saimiri sciureus* (*n*=29). Dark bars represent mixed-species sightings (*n*=8) and light bars for single-species sightings. Canopy levels follow Yoneda (1984) – 1: understory (0-5m), 2: Lower (5-10m), 3: Middle (10-20m), 4: Upper (20-30m). Neither *Sapajus* nor *Saimiri* were observed in the emergent canopy (≥30m).

Appendix IX. *Living Together post refurbishment initial report*

The data were collected, and the initial report was written by two MSc students (Meave Park and Amy Sanders) from the University of Stirling, who were working as research assistants as part of their placement. Data collection took place during January-March 2020 (data collection ended prematurely due to the COVID-19 pandemic).

During outdoor observations, substrate use by *Sapajus* and *Saimiri* of the new structures added as part of the refurbishment (see Figure 9.1) were recorded using continuous sampling methods (Martin & Bateson, 2007). Tallies were noted when *Sapajus* or *Saimiri* locomoted, sat or swung from each of the following substrates: boxes attached to trees (box 1 and 2), four mesh baskets atop trees (mesh 1-4), trees in the centre and around outskirts (not including bare tree branches that make up centre structure), feeding platforms, hose hammocks and ropes/vines connecting structures (including ropes near the houses and connecting houses to centre structure). See enclosure map below for clarification on numbered substrates.

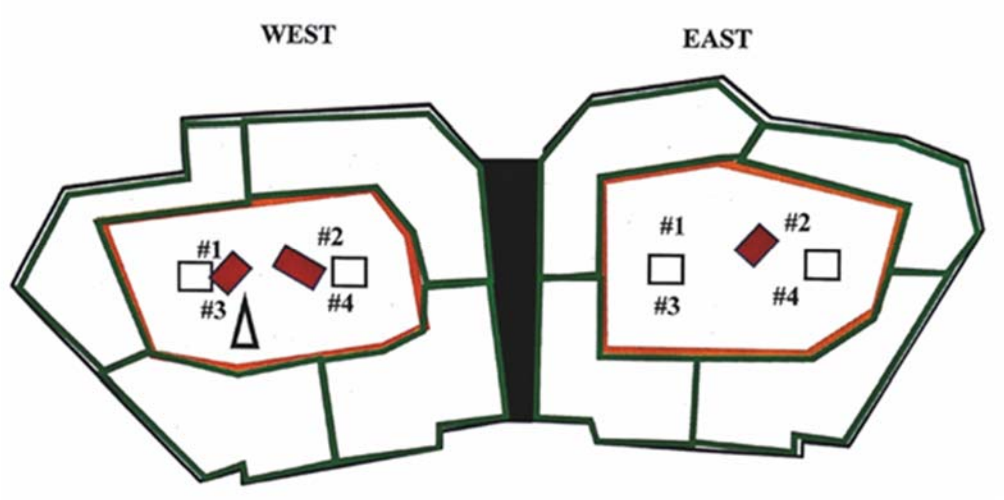

Figure 9.1 Schematic diagram of outdoor enclosures (not to scale), including the new substrates added as part of the refurbishment: white squares represent boxes 1 (left) and 2 (right), red squares represent hose hammocks, triangle represents swirl tree, #1-4 represents mesh baskets 1-4.

Indoor and Outdoor Enclosure Use

The East *Sapajus* were observed indoors and outdoors in fairly even proportions with just slightly more recorded using the outside space (52%) than inside (48%). The West *Sapajus* were observed using the outdoor space less, with just over double the number of individuals recorded indoors (indoor = 68%, outdoor = 32%) over the observation period. Both groups of *Saimiri* were observed using their indoor enclosure more than their shared outdoor enclosure, with both East and West groups spending around 90% of their time indoors (East = 89% and West = 96%). Squirrel monkeys on the East were observed to spend more time outdoors than on the West (East = 11% and West = 4%).

Substrate Use

Despite the difference in outdoor enclosure use between the East and West groups it would seem from Figure 9.2 that both *Sapajus* groups still make use of most of the new substrates when they were outside. Particularly, the boxes, ropes/vines and trees. Boxes were commonly used to shelter from wind/rain and but also allogrooming was often seen taking place in and on top of the boxes. Trees also seemed to be used for resting and/or taking shelter, while ropes and vines made good connections between different substrates. Play behaviour was often observed to be initiated on top of boxes and involved jumping between these and the feeding platforms, trees and ropes and vines. Solo play was also observed in the East group with individuals swinging from trees/branches as well as jumping into bamboo shoots. Hose hammocks and feeding platforms generally seemed to be used for foraging. *Sapajus* in the West group were never seen using the swirl tree, which was to be expected as it was placed there to encourage the *Saimiri* to move to other parts of the enclosure. Most substrates were used across all observation days with the exception of the mesh baskets which were only observed on days that tended to be sunny and warm, with the baskets being used for resting (and possibly sunbathing). Due to the majority of observation days taking place during cold and wet days this could explain the low frequency of use for the mesh baskets. Sunnier days where overall consistent with more outside and substrate use so it is likely increased use will be seen during the warmer summer months.

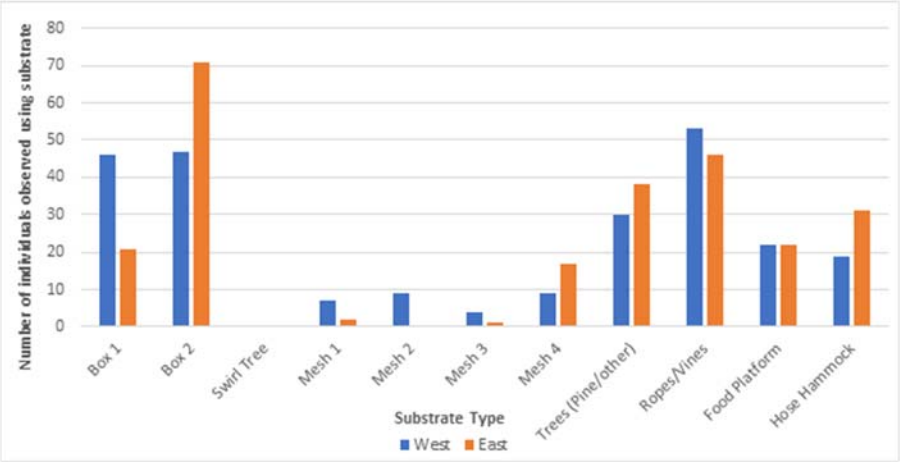

Figure 9.2 Frequency of *Sapajus* observed using each substrate for the East *n*=19 and West *n*=18 groups.

The substrate type used most often by both groups of *Saimiri* was the trees, with the East group observed almost a third more than those on the West (see Figure 9.3). The second most used substrates were the ropes and vines (see Figure 9.3). Similarly to previous findings (e.g. Daoudi, Badihi & Buchanan-Smith, 2017), there was a higher frequency of *Saimiri* using the substrates in the East group compared to the West group. The ropes and vines were used as a means of transportation to get to other substrates within the outdoor enclosure, mainly the trees. The trees were commonly used for resting in sunnier weather. On the West, a low frequency of *Saimiri* were observed using the mesh baskets (Mesh 3 & 4), however none from the East group were observed using these substrates (see Figure 9.3). Despite the swirly tree (only in the West enclosure), being placed in the enclosure specifically for *Saimiri*, they only used it during one day of observations, the substrate was seemingly used for rest and play, and the weather was clear and sunny. Only a low frequency of the East *Saimiri* were observed using the feeding platforms, as well as the hose hammocks, which the West *Saimiri* were also observed using (e.g. for foraging). The boxes were seldom used by either of the *Saimiri* groups. Furthermore, *Saimiri* were observed more frequently outside on sunnier days, therefore it is likely that substrate and outdoor use is weather dependent and is likely to increase during the summer months (i.e. when temperatures are warmer).

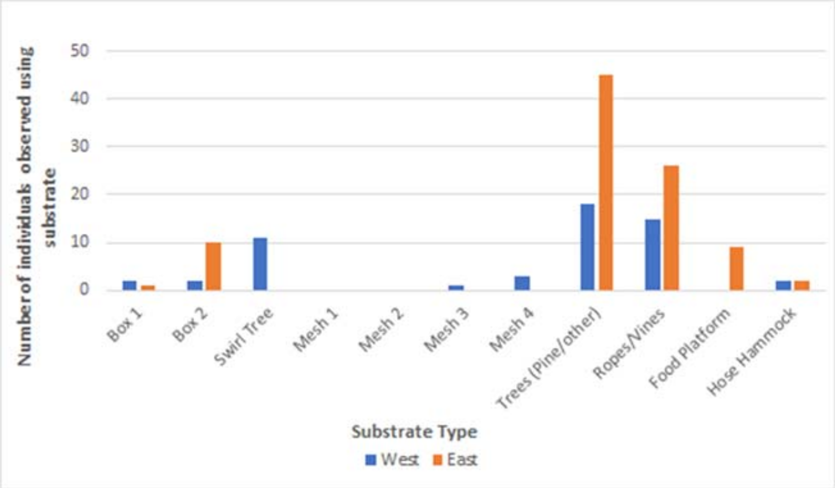

Figure 9.3 Frequency of *Saimiri* observed using each substrate for the East (*n*=17) and the West (*n*=15) groups.

Final points

As both *Sapajus* groups have access to similar substrates, it is not immediately clear why lower levels of outdoor use was seen in the West group compared with the East (though this is in keeping with previous findings, see Buchanan-Smith et al., 2013; Daoudi et al., 2017). However, overall the new substrates seem to be used well by both *Sapajus* groups with the substrates encouraging a variety of behaviours (resting, grooming, play). The percentage of observations where *Saimiri* were outdoors remained low, with the East groups outdoors slightly more often than the West. It seems that they are still occupying similar areas as before the refurbishment (however this may change during warmer weather).