

Buchanan-Smith HM, 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 (3-4), pp. 324-333.

This is the peer reviewed version of this article

NOTICE: this is the author's version of a work that was accepted for publication in Applied Animal Behaviour Science. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in Applied Animal Behaviour Science, [VOL 147, ISS 3-4 (2013)] DOI: <http://dx.doi.org/10.1016/j.applanim.2013.04.004>

Please e-mail h.m.buchanan-smith@stir.ac.uk for a personal copy of this article published in **Applied Animal Behaviour Science 147, 324-333 (2013)**

Interspecific interactions and welfare implications in mixed species communities of capuchin (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) over 3 years

Hannah M. Buchanan-Smith^{1*}, Joana Gričiute¹, Sophia Daoudi¹, Rebecca Leonardi¹ and Andrew Whiten²

¹ Behaviour and Evolution Research Group and Scottish Primate Research Group, Psychology, School of Natural Sciences, University of Stirling, Stirling, Stirlingshire, FK9 4LA, Scotland

² Centre for Social Learning, and Cognitive Evolution and Scottish Primate Research Group, School of Psychology, University of St. Andrews, St Andrews, Fife, KY16 9JP, Scotland

*Corresponding author.

Tel.: +44 01786 467674

Fax: +44 01786 467641.

E-mail address: h.m.buchanan-smith@stir.ac.uk (H.M. Buchanan-Smith).

ABSTRACT

Species have complex relationships with others in the wild, and some such as capuchin (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) naturally choose to associate with each other. There are a number of benefits of exhibiting such species in correspondingly mixed communities in captivity to enhance welfare through increased social complexity, which is potentially environmentally enriching in restricted captive enclosures. Monitoring the interactions between species is critical, however, particularly when members of one species are considerably larger and potentially more aggressive than the other. We report on the frequency and nature of interspecific interactions between *S. apella* and *S. sciureus* during four time periods over 3 years (2008-2010) following the formation of two mixed species groups at the 'Living Links to Human Evolution' Research Centre in Edinburgh Zoo, Scotland. Both the rate and the distribution of interspecific interactions among aggressive, affiliative and neutral categories of behaviour varied over time ($\chi^2=14.98$, $df=6$, $P<0.05$). We predicted that *S. apella* would engage in more interspecific, particularly aggressive, interactions than *S. sciureus* than *vice versa*, as they are the larger, more social species and have a more pugnacious temperament. This was the case overall ($t=3.3$, $df=3$, $P<0.05$), and particularly in 2009 and 2010. We predicted that affiliative interactions would increase over time as the number of youngsters increased and as the youngsters grew up together, establishing equitable relationships and "territorial" boundaries. The data did not support this prediction. Both the most affiliative and least aggressive interspecific interactions were observed following internal enclosure refurbishment in 2008 and hence we argue that good enclosure design and husbandry is the most important factor in promoting positive interactions between individuals in mixed species groups. We conclude that long-term monitoring is important, and when combined with appropriate husbandry and enclosure upkeep, the welfare of individuals is enhanced in mixed species groups by the presence of other species.

Key words: Mixed species group; interspecific interactions; enclosure design, capuchin, squirrel monkey, *Cebus*

1. Introduction

There are many components of animal welfare, and behaviour is an excellent indicator of an animal's overall welfare state. Behaviour is the ultimate phenotype – not only reflecting the animal's own individual decision making processes, it can also represent the expression of emotions (Darwin, 1982; Dawkins, 2004). Interspecific behaviour allows one to quantify the nature of relationships between individuals to determine their compatibility. As Dawkins (2004) notes, recording behaviour is non-invasive (e.g. does not require breaking the skin), and in many cases it is also non-intrusive (the animal may not be disturbed in any way). As such behavioural measures of welfare are ideal for many studies.

Poole (1992) described four 'behavioural needs' of mammals and discussed them in relation to their welfare in captivity. These needs are security, appropriate environmental complexity, novelty and opportunities for achievement. They are not necessarily required for immediate survival or reproduction (c.f. food, water, sex), but are critically important for good welfare. If such needs are met, individuals may exhibit characteristics of what Poole (1997, p 116) operationally defined as a 'happy animal': one which is 'alert and busy (displays a wide behavioural repertoire), is able to rest in a relaxed manner, is confident (outward going and does not display fear towards non-threatening stimuli) and does not display abnormal behaviour.'

Buchanan-Smith (2010) described how Poole's (1992) behavioural needs can be met through careful design of captive enclosures and appropriate environmental enrichment. Animal staff should aim to provide environments that encourage animals to perform a diversity of normal (wild, desired) behaviours, throughout the whole environment provided. Such environments should prevent abnormal behaviours from developing and allow animals to build resilience to cope with challenges they face (Buchanan-Smith, 2010). It is also helpful to consider concepts additional to Poole's four behavioural needs of security, environmental complexity, novelty, and opportunities for achievement - notably those of choice and

control and their relationship with predictability - in order to promote good welfare (Bassett and Buchanan-Smith 2007; Buchanan-Smith, 2010; Buchanan-Smith and Badihi, 2012).

The provision of appropriate environments generally focuses on physical aspects (e.g. enclosure size, furnishings), food enrichment (e.g. presentation, variety, processing), and cognitive/occupational enrichment (e.g. novel objects, foods puzzles), that may stimulate animal senses in a variety of ways (Buchanan-Smith, 2010). However, social enrichment is potentially the most important aspect for social species. Appropriate early social rearing is critical for developing skills and resilience in primates (Parker and Maestriperi, 2011). Interactions such as play and allogrooming contribute to positive emotions and hence improved welfare (Joint Working Group on Refinement, 2009). Companions can also buffer stress factors (e.g. Gust et al., 1994, Schaffner and Smith, 2005). Interactions with other animals can constantly change, providing a complex social situation, that may at times be unpredictable and socially challenging, and hence group dynamics require careful monitoring (Visalberghi and Anderson, 1993). Social enrichment is usually provided by compatible conspecifics but animals of other species also have the potential for improving animal welfare (Buchanan-Smith, 2012).

Housing individuals in mixed species groups is one such way to provide animals in zoos with complex social and physical environments, and is commonplace in many zoos (e.g. Veasey and Hammer, 2010 and see Sodaro, 2008 for a survey of mixed species housing of Neotropical primates). Mixed species exhibits have many potential benefits, particularly if the species naturally choose to associate in the wild (reviewed in Buchanan-Smith, 2012). The animals themselves are likely to be housed in a larger enclosure in mixed species exhibits than occurs in single species groups (e.g. Baker, 1992). The increases in physical activity observed (e.g. Buchanan-Smith, 1999; Heymann et al., 1996) and increased complexity and cognitive challenges may lead to improved welfare (Thomas and Maruska, 1996). Furthermore, zoo visitors may experience a more dynamic, interesting and more informative naturalistic exhibit than if the animals were housed in single-species groups. These are all key considerations in zoo design and management.

In this paper we describe the results of our behavioural observations on interactions between two species – brown capuchins (*Sapajus apella* formerly of taxonomic name *Cebus*, Alfaro et al., 2012) and common squirrel monkeys (*Saimiri sciureus*) housed at the ‘Living Links to Human Evolution’ Research Centre in Edinburgh Zoo, in relation to their welfare. These two species form natural associations in the wild, spending up to 50% of their time in temporary but stable mixed species groups, and moving together for a few hours or on occasion up to 12 days (Podolsky, 1990). *S. apella* lives in groups with an average size of about 17 conspecifics (averaged from various field sites, Fragaszy et al., 2004). *S. sciureus* lives in larger groups of 30-70 conspecifics (Mitchell, 1994; Terborgh, 1983) although Boinski et al. (2003) report a lower average group size of 23 conspecifics. As such large group sizes are unlikely to be attainable in the captive environment, exhibiting these two species together increases overall group size and as such promotes social complexity.

It is critical to consider enclosure design carefully, to distribute resources so the animals do not compete over them, and to provide behavioural choice (Buchanan-Smith, 2012). Captivity changes animal behaviour. In space-restricted enclosures, animals are in closer proximity than they would be in the wild. With provisioning by humans, they also spend less time foraging, and as there is no predation, their behaviour can change accordingly, leaving more time for both intra- and interspecific interactions. Whilst these interactions can be very positive, providing a complex physical enclosure and the ability to avoid both conspecifics and heterospecifics helps to fulfil the animals’ behavioural needs (Poole, 1992).

Monitoring interspecific interactions is particularly important as of all the naturally associating primate species, *S. apella* and *S. sciureus* have the highest relative difference in body size, with *S. apella* being much larger than *S. sciureus*. Adult male *S. sciureus* weigh only an average of 0.74kg, while *S. apella* males average 3kg (Jack, 2007). In addition, *S. apella* are known to prey upon a range of animals, including primates (Carretero-Pinzón et al., 2008; Sampaio and Ferrari, 2005) and other mammals (e.g. Galetti, 1990; Izawa, 1990; Resende et al., 2003; Terborgh, 1983) although we are not aware of any reports of *S. apella*

attacking *S. sciureus* in the wild or in captivity. Providing opportunities for choice so species may separate into different enclosure areas may be particularly important for the *S. sciureus*, to allow them to feel secure.

To determine the success of social enrichment in the mixed species exhibit, we collected data using identical methods, over four time periods in 3 consecutive years on two mixed species groups following their initial mixing. The study was designed to allow us to explore whether, and if so how, the nature of interspecific interactions change, and we describe this in relation to enclosure refurbishment, mixed species group size, and number of youngsters. Larger-bodied animals are generally dominant to smaller bodied animals, both intraspecifically (Maynard Smith 1979) and interspecifically (primates: Heymann and Buchanan-Smith, 2000), but individual and species temperament may also play a vital role. Although both species are gregarious and form close social relationships with conspecifics, unlike *S. apella*. *S. sciureus* almost never allogrooms (Baldwin and Baldwin, 1981; Fragaszy et al., 2004). Further, *S. apella* are characterised by boldness and pugnacity that is evident as initiation of aggressive interspecific interactions, particularly if defending resources (Rose et al., 2003). Interestingly Leonardi et al. (2010) found that both *S. apella* and *S. sciureus* exhibited a similar rate of intraspecific aggression in single species groups but *S. apella* decreased intraspecific aggression in mixed species groups (from around 0.33/hr to 0.1/hr). Given the size differential, the more pugnacious temperament of *S. apella* than *S. sciureus*, and that in this study *S. sciureus* often took food from the indoor *S. apella* enclosure (but the reverse was not possible), it was predicted that *S. apella* would initiate more interactions, particularly aggressive interactions, than *vice versa*.

We were also interested to determine whether interactions would differ in relation to the number of youngsters. Youngsters of both species may be particularly susceptible to aggressive interactions, and adults may be more protective when they have young (Hardie et al., 2003). However, at Living Links, Leonardi et al. (2010) found that compared with adults, youngsters initiated more interspecific affiliative

and neutral interactions than expected by chance. As the number of youngsters increased over time, and youngsters grew up together, we predicted an increase in affiliative interactions and that less aggression would be observed as “territorial” boundaries between the species were established. By “territorial” we refer to a preferred area of the enclosure which one species will defend against the other if they attempt to enter it. This included resources such as wide horizontal branches that *S. apella* preferred to rest upon, and feeding stations in the *S. apella* indoor enclosures. We also explored changes in the nature of interspecific interactions following enclosure refurbishment (data partially published in Leonardi et al., 2010) and set these data in the longer-term context.

2. Methods

2.1 Study Animals, Housing and Husbandry

We studied two mixed species groups of brown capuchin (*Sapajus apella*, formerly of taxonomic name *Cebus*, Alfaro et al., 2012) and common squirrel monkey (*Saimiri sciureus*) housed at the ‘Living Links to Human Evolution’ Research Centre, situated within the Royal Zoological Society of Scotland’s Edinburgh Zoo (UK). The Centre was opened in May 2008 and our research spans four time periods over 3 consecutive years from 2008-2010. Enclosures for the two mixed species groups mirror each other and are named the ‘West’ and ‘East’ wings (Leonardi et al., 2010; MacDonald and Whiten, 2011). Each wing includes an indoor *S. sciureus* enclosure (5.5m x 4.5m x 6m high), to which only the *S. sciureus* are small enough to gain access, giving them control over when to associate, an indoor *S. apella* enclosure (7m x 4.5m x 6m high) which both species are able to enter, and a large shared outdoor enclosure of approximately 900m² (Leonardi et al., 2010). There are three exit/entrance routes between each indoor enclosure and the outer enclosures. Both species have free access between inner and outer enclosures except during routine husbandry such as cleaning and by request of researchers (Leonardi et al., 2010; MacDonald and Whiten, 2011). Video footage which shows the size and furnishings of the Living Links

enclosures, describes the importance of choice, and clearly illustrates that individuals choose to be in proximity with members of the other species is available at

<http://www.youtube.com/watch?v=fAksjSUmaWk>.

Daily routines were similar for all four observation periods, as detailed by Leonardi et al. (2010). There was the main morning and afternoon feed, and three to four scatter feeds distributed throughout the rest of the day. The diets for the two species were similar, but when fed indoors differed in size of items, amounts given and frequency of feeding particular foods between the two species. Food included a variety of chopped fresh fruits, vegetables, primate pellets, hard-boiled eggs, chicken, insects, and larvae (mealworms, locusts, crickets, etc., typically twice daily for *S. sciureus* in scatter feeds and at least twice a week for *S. apella*) and vitamin supplements (sprinkled on feed). Scatter feeds also include mixed seeds, nuts, raisins, and dates. Most food items were small, and could be carried by individuals of either species. Feeding stations in indoor enclosure could be monopolized by dominant individuals. Water was constantly available in automatic drinkers in the indoor enclosures and holding cages (Leonardi et al., 2010).

Data were collected during four time periods over 3 consecutive years (2008, 2009 and 2010) during July and August. Across the 3 years of studies, there were no major changes to the overall structure of indoor or outdoor enclosures. Following initial data collection in Phase 1 of 2008, observations were made in Phase 2 (refurbishment) following changes to the internal enclosure furnishings to improve their use, provide better resting/sleeping areas, reduce competition over preferred areas as well as improve access to feed sites, and improve ability for individuals to avoid con- and heterospecifics should they choose to (see Leonardi et al., 2010). As *S. apella* are particularly destructive, the enclosure required regular maintenance over the next four years but none was done directly before or during the 2009 or 2010 data collection. A major refurbishment of all the internal and external furnishings was required by 2012, replacing the major supports which had gradually deteriorated, and providing an improved structural network.

The number and group composition of the West and East Wing inhabitants changed across the 3 years of study (see Table 1). There were the fewest youngsters in 2008 (six in each wing), with 9-11 youngsters in both subsequent years as the groups reproduced successfully. The total number of individuals observed each year varied from 22 to 24 in the West and 15 to 26 in the East. Only in 2010 in the West group was the ratio of *S. apella* to *S. sciureus* higher. Numbers varied as individuals were removed for husbandry purposes, to prevent intraspecific aggression or inbreeding, but each group contained several of the same individuals over the 3 years of data collection.

2.2 Procedure

Ad libitum sampling was used to record all occurrences of interspecific interactions using a set format recorded directly to Dictaphone (following Leonardi et al., 2010). Observations were divided equally between West and East wings, were made in both indoor and outdoor shared areas. In 2008, 64h of data were collected by RL split into two phases (39h in Phase 1 pre- refurbishment; 25h in Phase 2, post-refurbishment – refurbishment is described above). These 2008 data were collected shortly after relocation to the new Living Links Centre and mixed species group formation (see Dufour et al., 2011). Identical data collection methods were used in 2009 (42h by SD) and 2010 (20h by JG). Inter-observer reliability (IOR) was assured by observers learning from each other and the project leader (HMB-S) whilst observing the monkeys, and detailed unambiguous descriptions being available. No formal IOR calculations were feasible on each interaction type due to low occurrence. Rates per hour of all interspecific interactions were calculated but it is noted that these are an underestimate of true rates as the monkeys were distributed throughout several enclosures while the observer could only view one enclosure at any time (Leonardi et al., 2010). However, the ratio of aggressive:affiliative:neutral interactions is unaffected by this limitation and allows comparison of the distribution of the nature of interactions between time periods and groups. When recording interspecific interactions, we noted the details of the event, the type

of interaction, along with the direction of the interaction, the response to it, and when possible, the individuals involved (Tables 2-4 following Leonardi et al., 2010). Only categories observed more than once are detailed. Individual *S. sciureus* were identified by colour coded beads on necklaces; *S. apella* were distinctive enough without the aid of identification markings. Rates of interaction type, per individual (excluding carried infants), per hour were calculated and correlated (Pearson) with number of young. Paired sample t-tests were used to compare species in the rate of interactions per hour. Scan data taken at ≥ 15 min intervals were collected in 2008 and 2009 to provide an estimate of the percent of time spent in shared enclosure areas. All data collection for this study was conducted when no husbandry or research activity (e.g. positive reinforcement training or cognitive testing) was in process. The research was approved by the University of Stirling Psychology Ethics Committee and abided by the Association for the Study of Animal Behaviour Ethical Guidelines (ASAB, 2006).

3. Results

3.1 *The rate of interspecific interactions and type of interactions across years*

Individuals of both species spent an estimated 80% of their time in the shared indoor and outdoor enclosure areas together (2008 and 2009 scan data), and the *S. sciureus* used the *S. apella* indoor enclosure across all 3 years in both West and East wings. There was variation in the total number and type of interspecific interactions (West and East combined) across the four periods of observations. In 2008 Phase 1, there was a rate of 2.5 interactions/hr, similar to Phase 2 at 2.2/hr. In 2009 the rate decreased to 1.1/hr but in 2010, the rate returned to 2008 levels (2.4/hr). We predicted that affiliative interactions would increase over time and that less interspecific aggression would be observed as “territorial” boundaries between the species were established (see Introduction). The percentage of observations of aggressive, affiliative and neutral interactions are presented in Fig. 1 (West and East separately) and Fig. 2 (combined data). During the four time periods of observations the frequencies of the types of interspecific

interactions varied significantly ($\chi^2=14.98$, $df=6$, $P<0.05$). Pairwise comparisons of time periods indicated that only Phase 1 and 2 (pre- and post-refurbishment) were significantly different from each other in types of interspecific interactions ($\chi^2=6.1$, $df=6$, $P<0.05$). Aggressive interactions decreased and affiliative interactions increased from Phase 1 to Phase 2 whilst neutral interactions occurred at a similar level. To take changes in group size into account, the rate per individual per hour of each type of interaction was calculated for West and East groups separately across the time periods. Contrary to our prediction that affiliative interactions would increase with the number of youngsters in the group, the rate/ind/hr of affiliative interactions was significantly negatively correlated with the number of youngsters in the mixed species group ($r = -0.82$, $n=8$, $P<0.05$). There was no significant correlation between the rate/ind/hr of aggressive interactions and the number of youngsters ($r=-0.20$, $n=8$, $P>0.05$), nor for neutral interactions ($r=-0.6$, $n=8$, $P>0.05$). There was no correlation of total mixed species group size and rate/ind/hr of affiliative ($r=-0.62$, $n=8$, $P>0.05$) and aggressive ($r=-0.53$, $n=8$, $P>0.05$) interactions, but neutral interactions were significantly negatively correlated ($r=-0.83$, $n=8$, $P\leq 0.01$). The ratio of *S. apella* to *S. sciureus* was higher only in 2010 in the West group but the proportion of aggressive interactions did not change (see Fig. 1).

3.2 The range and frequencies of types of interactions and responses to them

The frequencies of types of aggressive, affiliative and neutral interactions are presented in Table 4. The types of aggression observed differ for each year: 'displace non-contact' and 'vocal exchange' were observed only in 2008 (both phases) and 2009, and not in 2010. In 2009 'chase no contact' was the most commonly observed aggressive interaction, but in 2010, most of the aggressive interactions included physical contact during the chase. The responses to the interactions were usually to "move away" but in 2010, the response to the aggressive interactions had changed to aggression, with and without contact (Table 4).

The types of affiliative interactions also varied across the years. In 2008 Phase 2, there was the greatest breadth of types of interactions (despite fewer hours of observation than in Phase 1 or 2009), with 'curious approach' and 'play' dominating in the other years. Initiation of affiliative interactions was usually met with 'approach' or 'unconcerned' in 2008 (both phases), but in 2009 and 2010 the response was most often to 'move away'. Twice in 2009 the monkeys responded to affiliative initiation with 'aggression'. 'Close proximity-no contact' dominated all neutral interactions across the years.

The most common reason for aggressive interactions was 'territorial' across all years except Phase 2 in 2008 (Table 4). 'Assert dominance' and 'food resource' were the next most common. The most frequently observed reasons for affiliative interactions during the 3 years were 'curious' and 'playful' across all years. Only in 2008 Phase 2, was 'relaxed/comfortable' observed as one of the reasons for affiliative interactions. Neutral interactions showed a breadth of reasons recorded in 2008 and 2010, but 'access to area' was the only reason recorded in 2009.

3.3 The direction of interspecific interactions

As predicted the larger and more pugnacious species, *S. apella* initiated more aggressive interactions than *S. sciureus*. The rate/ind/hour was significantly higher for *S. apella* than *S. sciureus* ($t=3.3$, $df=3$, $P<0.05$). *S. apella* also initiated significantly more neutral interactions than *S. sciureus* ($t=3.7$, $df=3$, $P<0.05$) but the frequency of initiation of affiliative interactions did not differ between species ($t=2.6$, $df=3$, $P>0.05$; see Table 5).

Using the raw data to explore the relationship with time, a Chi square revealed a significant relationship between time period and direction of aggressive interactions ($\chi^2=17.4$, $df=3$, $P\leq 0.001$). There is clear pattern underlying the direction. In 2008 Phase 1 and 2 both species initiated aggressive interactions almost equally but this pattern was significantly different to 2009 ($\chi^2=7.21$, $df=3$, $P<0.01$) and 2010

($\chi^2=13.2$, $df=3$, $P<0.001$) when *S. apella* initiated more than *S. sciureus*; the pattern of direction of aggressive interactions in 2009 and 2010 was not significantly different ($\chi^2=3.14$, $df=3$, $P>0.05$).

The pattern of initiation of affiliative interactions was also significantly related to time period ($\chi^2=15.2$, $df=3$, $P<0.01$). In 2008 *S. apella* were almost equally likely to initiate affiliative interactions as *S. sciureus* (31 to 25, and were not significantly different in Phase 1 and 2) but by 2010, *S. sciureus* never initiated affiliative interactions (c.f. 2008, $\chi^2=12.3$, $df=1$, $P<0.01$). Neutral interactions were initiated more by *S. apella* across all years, but were not significantly related across the four time periods ($\chi^2=6.02$, $df=1$, $P>0.05$ (see Table 5).

4. Discussion

Primates in captivity are often considered to require more attention than other animals in order to meet their behavioural and welfare needs. Our data illustrate the complex and constantly changing dynamics of interspecific interactions in two mixed species communities and the need for such studies to monitor behaviour relevant to welfare concerns. Whilst care must be taken when introducing species to each other to initially form such groups (see Buchanan-Smith 2012 for a list of factors to consider), our data documenting changes over time show the importance of long-term monitoring, as the nature of interactions can change substantially. Following initial introductions (Phase 1), interspecific interactions were equally distributed across aggressive, affiliative and neutral categories, and *S. sciureus* initiated as many interactions as *S. apella* (although the rate/ind/hr for *S. sciureus* was significantly lower than *S. apella* throughout). In 2009 and 2010 *S. sciureus* hardly ever initiated interactions, and indeed there was a significant negative correlation between the rate of neutral interactions and mixed species group size. This suggests that *S. sciureus* were avoiding rather than seeking out interactions with *S. apella*, although they continued to use all enclosure areas. Analyses of affiliative interactions in 2009 and 2010 indicate that

although species continued to do 'curious approach' and 'play' with each other, these were initiated more by *S. apella*, and were occasionally responded to with aggression by *S. sciureus*.

Further circumstantial evidence that the nature of interspecific relationships changed from *S. sciureus* seeking out *S. apella* comes from the finding that in 2008 only, in the West group, did a subgroup of *S. sciureus* sleep in the *S. apella* enclosure (Leonardi et al., 2010), suggesting the *S. sciureus* felt secure in the presence of *S. apella* as sleeping is a particularly vulnerable time. In the East group also, early interactions were mostly positive, particularly following internal enclosure refurbishment (see Leonardi et al. 2010) but in 2009 and 2010, half of all the interactions were aggressive, which included contact aggression, and the responses were also aggressive, even to affiliative approaches. The reasons for increases in aggressive interactions were not associated with changes in group size, nor number of youngsters in the group, which might have been the case if they were specific targets of such interactions. The only consistent pattern of change in the nature of interactions across both West and East groups was from pre- to post-refurbishment so we conclude that this had the most important effect on the nature of interactions.

It must also be noted that aggression is not necessarily poor for welfare. Aggression is natural, and promotion of natural behaviour is a goal of environmental enrichment as long as it is not detrimental to animal health (Buchanan-Smith, 2010; Young, 2003). No injurious interspecific interactions were ever observed, but contact aggression may have lead to *S. sciureus* avoiding the *S. apella*, with the potential for chronic social stress as has been suggested in other mixed species primate exhibits (e.g. Dalton and Buchanan-Smith, 2005). However, it may also be, with careful enclosure design, that such seemingly negative interactions are cognitively stimulating. The brains of most primates are larger (in relation to body size) than other mammals (e.g. Dunbar and Schultz, 2007). Being socially vigilant, and learning to avoid key aggressive individuals, may provide a prime reason to exercise these large brains. There are a number of competing hypotheses for the evolution of large brain size in primates (reviewed in Healy and Rowe, 2007)

that primarily focus on dealing with the complexity of social and physical worlds. Providing appropriate early environments and such physical and social complexities in captivity can be very challenging, given the management difficulties of mimicking natural group size and structure. However, it is critical to find ways to introduce such complexity to minimise boredom, apathy, fear and other negative welfare states, and promote positive welfare states of security, with opportunities for achievement (Poole, 1992).

Housing naturally-associating species in mixed exhibits is one such way to improve both social and physical complexity. Living Links was built specifically for *S. apella* and *S. sciureus*, and the design took into account a considerable number of factors that included ecological differentiation, different locomotor patterns and preferred support orientations and size, as well as differences in diet. Although several factors changed over the years (group size, number of youngsters, ratio of *S. apella* to *S. sciureus*), only internal enclosure refurbishment targeted at minimising aggressive intra- and interspecific interactions (see Methods) improved the nature of interactions consistently in both groups. As such, and given the difficulties of predicting how individuals may interact, providing a separate enclosure for *S. sciureus*, which the *S. apella* could not enter, was critical in giving them choice to avoid *S. apella*, and for providing them with an area where they could feel secure. In addition to the social interactions, *S. sciureus* may benefit from association with the more destructive *S. apella*, and they have been observed getting access to otherwise unavailable food in Living Links made available by *S. apella* (Leonardi et al., 2010). Indeed, enrichment that encourages both species to interact is regularly provided (see <http://www.youtube.com/watch?v=fAksjSUMaWk>). Our findings emphasise the importance of formal data collection and informal monitoring to ensure that intentionally bringing the two species into close contact is not detrimental to their welfare. Future research may consider using Waser's (1980) gas model to determine whether movements of apparently associating animals are random or not (e.g. as used by Buchanan-Smith, 1990), and combined with social network analyses (e.g. Wey et al., 2008) a fuller understanding of the changing nature of the interspecific relationship could be achieved.

As Living Links is both a research centre and a public engagement with science centre (Bowler et al., 2012; MacDonald and Whiten, 2011) it is also important to consider the methodological implications of our findings for research. In addition to studies on the welfare of the monkeys in mixed species groups, there is research on, for example, cognitive ability, social learning and social networks. Our findings suggest that enclosure furnishings affect interactions amongst species, and therefore deterioration of, or changes to furnishings may confound research findings on social interactions and behaviour. This may be particularly relevant to studies on social networks and interspecific social learning. Furthermore, if animals have to maintain high vigilance to ensure they can avoid key individuals, this may impact on their ability to attend to cognitive tasks provided and on their learning ability.

5. Conclusions

With the provision of increasingly complex and challenging environments, the need to carefully monitor the welfare of animals in mixed species exhibits is critically important. However with careful enclosure design, and the provision of choice to allow potentially more vulnerable species to take refuge, mixed species exhibits are an excellent way to enrich the lives of the inhabitants, whilst simultaneously providing a more informative and interesting display for visitors.

Conflict of interest

The authors of this manuscript have no conflict of interest that would inappropriately bias this research.

Acknowledgements

We thank Charlotte MacDonald, Alison Bates, Dee Masters and the staff at Living Links for careful husbandry of the monkeys, and Valerie Dufour for her input to the study design. The research was funded by Psychology, School of Natural Sciences, University of Stirling and the Living Links to Human Evolution Research Centre was

funded by a Strategic Research and Development Grant from the Scottish Funding Council. The research was approved by the University of Stirling Psychology Ethics Committee and adhered to the legal requirements in the United Kingdom. We thank two anonymous referees, and in particular Dr Steve Ross, for constructive comments that improved the manuscript.

References

- Alfaro, J.L., de Sousa E. Silva Jr., J., Rylands, A.B., 2012. How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. *Am. J. Primatol.* 74, 273–286.
- ASAB, 2006. Guidelines for the treatment of animals in behavioural research and teaching. *Anim. Behav.* 71, 245-253.
- Baker, B., 1992. Guess who's coming to dinner: an overview of mixed-species primate exhibits. *AAZPA Regional Conference Proceedings* 62–67.
- Baldwin, J.D., Baldwin, J.I., 1981. The squirrel monkeys, genus *Saimiri*. In: Coimbra-Filho, A.F., Mittermeier, R.A. (Eds.) *Ecology and behavior of Neotropical primates*, vol. 1. Rio de Janeiro: Academia Brasileira de Ciencias. p 277–330.
- Bassett, L., Buchanan-Smith, H. M., 2007. Effects of predictability on the welfare of captive primates. In: Swaisgood, R.R. (Ed.) *Animal Behaviour, Conservation and Enrichment*. *Appl. Anim. Behav. Sci.* 102, 223-245.
- 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*). *Behav.* 140, 1421-1467.
- 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(4):e34505.doi:10.1371/journal.pone.0034505
- Buchanan-Smith, H.M., 1990. Polyspecific association of two tamarins species, *Saguinus labiatus* and *Saguinus fuscicollis*, in Bolivia. *Am. J. Primatol.* 22, 205-214.
- Buchanan-Smith, H.M., 1999. Exploration of unfamiliar areas and detection of potentially threatening objects in single- and mixed-species groups of tamarins. *Int. J. Comp. Psychol* 12, 2–20.
- Buchanan-Smith, H.M., 2010. Environmental Enrichment for Primates in Laboratories. *Adv. in Sci. Res.* 5, 41-56.

- Buchanan-Smith, H.M., 2012. Mixed-species exhibition of Neotropical primates: Analysis of species combination success. *Int. Zoo Yearb.* 46,150-163.
- Buchanan-Smith, H.M. Badihi, I., 2012. The psychology of control: Effects of control over supplementary light on welfare of marmosets. *Appl. Anim. Behav. Sci.* 137, 166–174.
- Carretero-Pinzón, X., Defle, T. R., Ferrari, S. F., 2008. Observation of black-capped capuchins (*Cebus apella*) feeding on an owl monkey (*Aotus brumbacki*) in the Colombian Llanos. *Neotrop. Primates* 15, 62–63.
- Dalton, R., Buchanan-Smith, H.M., 2005. A mixed-species exhibit of Goeldi's monkeys and pygmy marmosets (*Callimico goeldii* and *Cebuella pygmaea*) at Edinburgh Zoo. *Int. Zoo Yearb.* 39, 176-184.
- Darwin, C., 1872/1965. *The expression of the emotions in man and animals*. Chicago: Univ. of Chicago Press.
- Dawkins, M.S., 2004. Using behaviour to assess welfare. *Anim. Welf.* 12, S3-7.
- 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. *Am. J. Primatol.* 73, 1-10.
- Dunbar, R.I.M., Schultz, S., 2007. Understanding primate brain evolution. *Phil. Trans. R. Soc. B* 362, 649–658.
- Fragaszy, D.M., Visalberghi, E., Fedigan, L.M., 2004. *The complete capuchin: The biology of the genus Cebus*. Cambridge: Cambridge University Press.
- Galetti, M., 1990. Predation on the squirrel, *Sciurus aestuans*, by capuchin monkeys, *Cebus apella*. *Mammalia* 54, 152–154.
- Gust, D.A., Gordon, T.P., Brodie, A.R., McClure, H.M., 1994. Effect of a preferred companion in modulating stress in adult female rhesus monkeys. *Physiol. Behav.* 55, 681–684.
- Hardie, S.M., Prescott M.J., Buchanan-Smith, H.M., 2003. Ten years of tamarin mixed-species troops at Belfast zoological gardens. *Primate Rep.* 65, 21–38.
- Healy, S.D., Rowe, C., 2007. A critique of comparative studies of brain size. *Proc. R. Soc. B* 274, 453-464.
- 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 Garten* 66, 381–390.

- Heymann, E.W., Buchanan-Smith, H.M., 2000. The behavioural ecology of mixed-species troops of callitrichine primates. *Biol. Rev. Cambridge Phil. Soc.*, 75, 169-190.
- Izawa, K., 1990. Rat predation by wild capuchins (*Cebus apella*). *Field Studies on New World Monkeys, La Macarena, Colombia* 3, 19–24.
- Jack, K.M., 2007. The Cebines: Toward an explanation of variable social structure. In: Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M., Bearder, S.K. (Eds). *Primates in Perspective*. New York: Oxford University Press, pp 107–123.
- Joint Working Group on Refinement (JWGR), 2009. Refinements in husbandry, care and common procedures for non-human primates: Ninth report of the BVA/AFW/FRAME/RSPCA/UFAW Joint Working Group on Refinement (M. Jennings & M.J. Prescott, Eds). *Lab. Anim.* 43 (Suppl 1): S1:1–S1:47
- 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*). *Am. J. Primatol.* 72, 33–47.
- MacDonald, C., Whiten, A., 2011. The ‘Living Links to Human Evolution’ Research Centre in Edinburgh Zoo: A new endeavour in collaboration. *Int. Zoo Yearb.* 45, 7–17.
- Maynard Smith, J., 1979. Game theory and the evolution of behaviour. *Proc. R. Soc. Lond., Series B*, 205, 475–488.
- Mitchell, C.M., 1994. Migration alliances and coalitions among adult male South American squirrel monkeys (*Saimiri sciureus*). *Behav.* 130, 169–190.
- Parker, K.J., Maestriperi, D., 2011. Identifying key features of early stressful experiences that produce stress vulnerability and resilience in primates. *Neurosci. Biobehav. Rev.* 35, 1466–1483.
- Podolsky, R.D., 1990. Effects of mixed-species association on resource use by *Saimiri sciureus* and *Cebus apella*. *Am. J. Primatol.* 21, 147–158.
- Poole, T. B., 1992. The Nature and Evolution of Behavioural Needs in Mammals. *Anim. Welf.* 1, 203-220.
- Poole, T., 1997. Happy animals make good science. *Lab. Anim.* 31, 116–24
- Resende, B.D., Greco, V.L.G., Ottoni, E.B., Izar, P., 2003. Some observations on the predation of small mammals by tufted capuchin monkeys (*Cebus apella*). *Neotrop. Primates* 11, 103–104.

- Sampaio, D.T., Ferrari, S.F., 2005. Predation of an infant titi monkey (*Callicebus moloch*) by a tufted capuchin (*Cebus apella*). *Folia Primatol.* 76, 113–115
- Schaffner, M., Smith, T.E., 2005. Familiarity may buffer the adverse effects of relocation on marmosets (*Callithrix kuhlii*): Preliminary evidence. *Zoo. Biol.* 24, 93–100.
- Sodaro, V., 2008 Survey on mixed species housing of Neotropical primates. Unpublished document.
- Terborgh, J., 1983. Five New World primates. Princeton, NJ: Princeton University Press.
- Thomas, W.D., Maruska, E.J., 1996. Mixed species exhibits with mammals. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.) *Wild mammals in captivity: Principles and techniques*: Chicago, IL: University of Chicago Press, pp. 204–211.
- Veasey, J., Hammer, G., 2010. Managing captive mammals in mixed-species communities. In: Kleiman, D.G., Thompson, K.V., Kirk Baer, C. (Eds), *Wild mammals in captivity: Principles and techniques*. Chicago, IL: University of Chicago Press. pp. 151–161.
- Visalberghi, E., Anderson, J.R., 1993. Reasons and risks associated with manipulating captive primates' social environments. *Anim. Welf.* 2, 3–15.
- Waser, P.M., 1982. Polyspecific associations: Do they occur by chance? *Anim. Behav.* 30, 1-8.
- Wey, T., Blumstein, D.T., Shen, W., Jordan, F., 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* 75, 333-344.
- Young, R.J., 2003. *Environmental enrichment for captive animals*. Oxford: Blackwell Science.

Fig. 1. Percentage of interaction types in two mixed species groups (labelled West and East) of *S. apella* and *S. sciureus* across 3 years: 2008 Phase 1 pre-refurbishment (n=98 in 39hr observations combined across groups), Phase 2 post-refurbishment (n=54 in 25hr), 2009 (n=47 in 42hr) and 2010 (n=48 in 20hr).

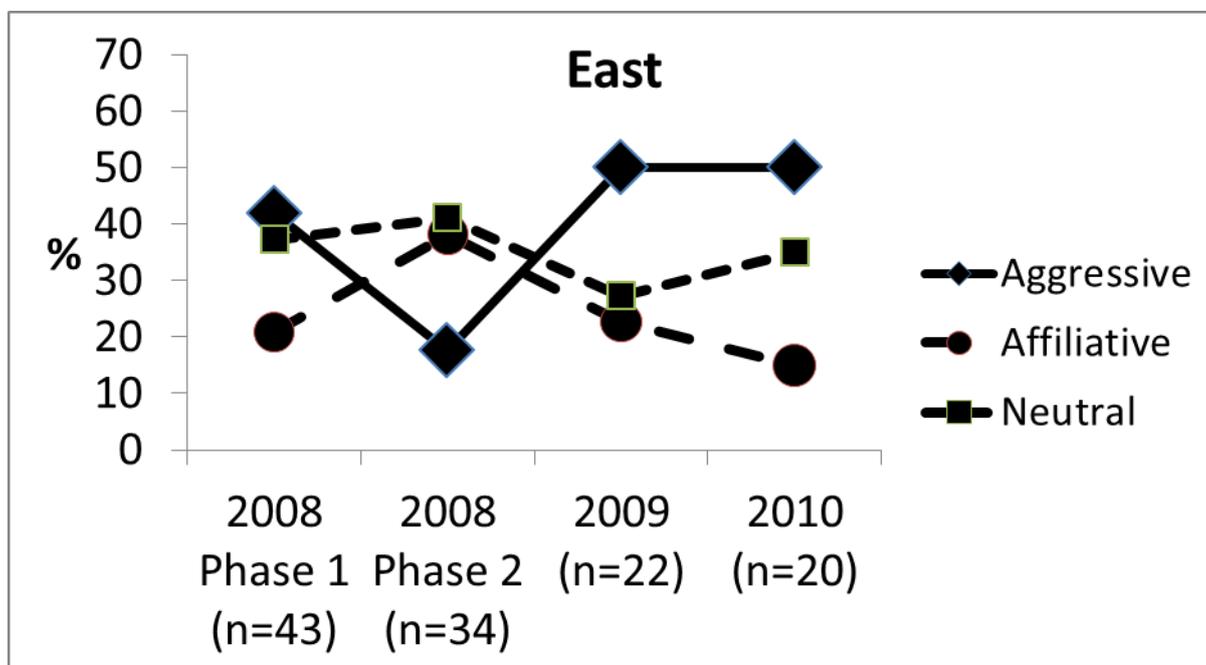
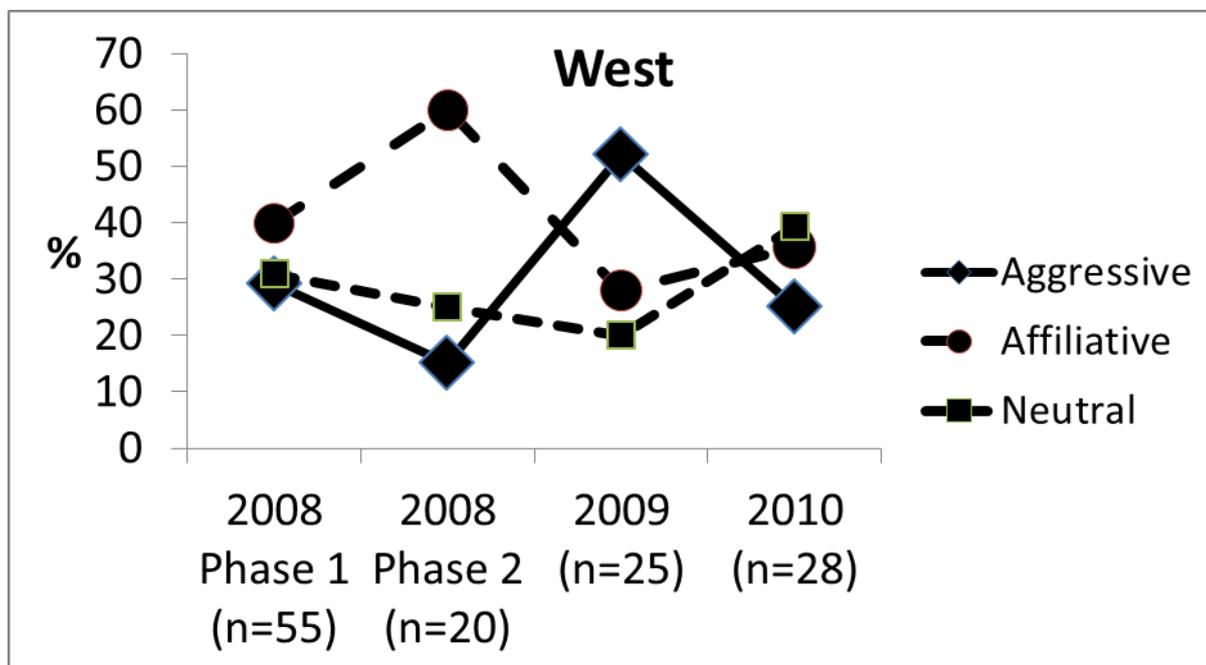


Fig. 2. Distribution of interspecific interaction categories for two mixed species groups of *S. apella* and *S. sciureus* across 3 years: 2008 Phase 1 pre-refurbishment (n=98 in 39hr observations combined across groups), Phase 2 post-refurbishment (n=54 in 25hr), 2009 (n=47 in 42hr) and 2010 (n=48 in 20hr).

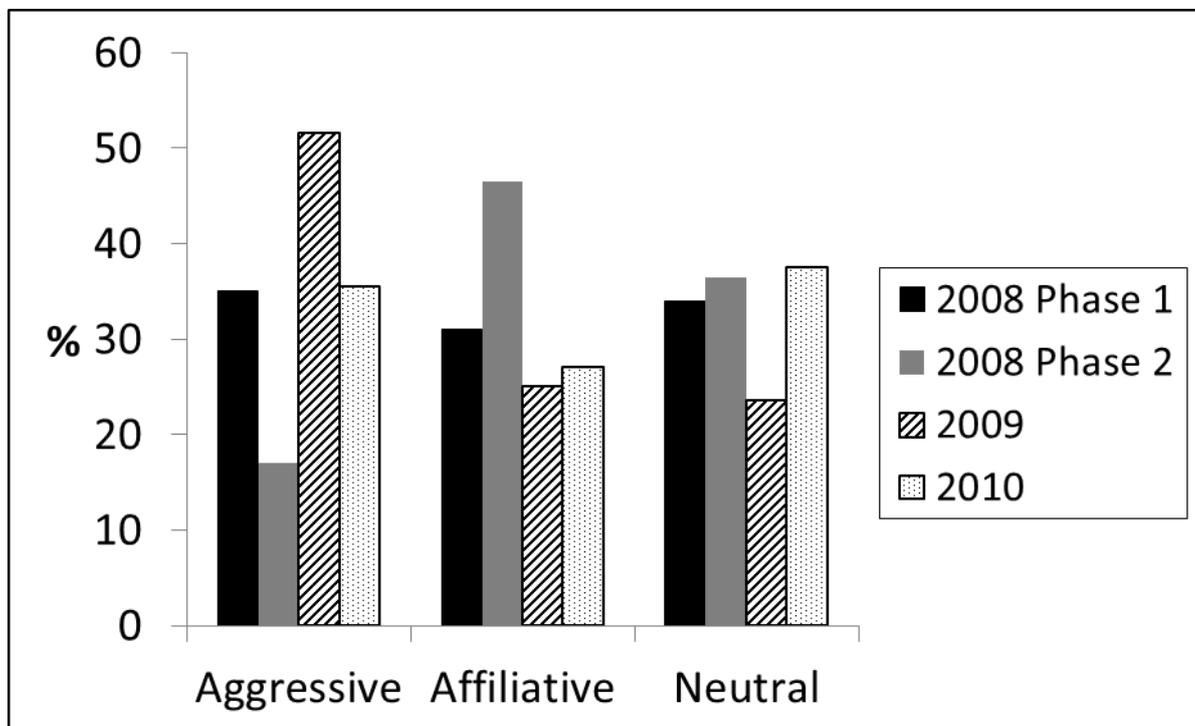


Table 1. Composition and size of the two mixed species groups in the West and East communities (number of youngsters in brackets), with ratio of *S. apella* to *S. sciureus*, over the 3 years of study. Individuals were categorized as youngsters at <4 years in *S. apella* and <2 years in *S. sciureus*. Infants are < 8 months (following Leonardi et al. 2010).

Year	West <i>S. apella</i>	West <i>S. sciureus</i>	East <i>S. apella</i>	East <i>S. sciureus</i>
2008	3 adult females 2 young males 1 male infant 1 carried infant Total 7 Phase 1 (2 y) Total 8 Phase 2 (2 y) + 1 adult alpha male	1 adult male 7 adult females 3 young males 1 young female 3 male infants Total 15 (4 y)	1 alpha male 1 adult female 3 young males Total 5 (3 y)	1 subadult alpha male 6 adult females 2 male infants 1 female infant Total 10 (3 y)
<i>S. apella:</i> <i>S. sciureus</i>	1 : 2.14 (Phase 1) 1 : 1.88 (Phase 2)		1 : 2	
2009	1 alpha male 2 adult males 3 adult females 2 young males 1 young female Total 9 (3 y)	1 alpha male 7 adult females 4 young males 3 young females Total 15 (7 y)	1 alpha male 2 adult males 2 adult females 2 young males 1 young female Total 8 (3 y)	1 alpha male 6 adult females 4 young males 4 young females Total 15 (8 y)
<i>S. apella:</i> <i>S. sciureus</i>	1 : 1.67		1 : 1.88	
2010	1 alpha male 2 adult males 3 adult females 5 young males 1 young female Total 12 (6 y)	1 alpha male 6 adult females 2 young males 1 young female Total 10 (3 y)	1 alpha male 3 adult males 3 adult females 2 young males Total 9 (2 y)	1 alpha male 7 adult females 6 young males 3 young females Total 17 (9 y)
<i>S. apella:</i> <i>S. sciureus</i>	1 : 0.83		1 : 1.89	

Table 2. Definitions of types of interspecific interactions by category (following Leonardi et al., 2010).

Interaction type	Definition
<i>Aggressive</i>	
Chase—no contact	One or more monkeys actively pursues one or more monkeys of the other species, moving at a rapid pace but not physically touching
Chase—contact	As above but physically touches (e.g. grabs/pinches)
Displace—non-contact	Monkey(s) approaches member(s) of other species at a walking pace causing the other species to move from its immediate area, but without making physical contact
Vocal exchange	Member(s) of different species face each other and call/shriek/scream, often accompanied by facial grimaces and retracted lips
Threat display	Monkey(s) engages in nonvocal aggressive behaviors toward member(s) of the other species such as genital displays (<i>S. sciureus</i>), facial grimaces (retracted lips, mouth open in <i>S. apella</i>), branch shaking, or rapid body movements in their direction (thrusting head forward then pulling back). No physical contact is made
<i>Affiliative</i>	
Play and play elicitation	Monkey plays with member(s) of the other species or attempts to elicit play with member(s) of the other species. Also includes attempts to join in intraspecific play, for example, moving close and engaging in similar play behaviors
Food beg	Monkey(s) make gestures to member(s) of other species holding an edible item, for example, arm extended with outstretched hand, palm facing upwards or reaching toward food item while in the other monkey's hand
Curious approach	Monkey moves toward member(s) of other species at a slow pace and does not display any aggressive behavior, but shows interest in other individual or initiates interaction (e.g. sniffing, gentle touch, or moving into <50 cm and observing)
Moving together	Individuals of both species travel in the same direction in close proximity (<2m) for an extended period (>2 min). Appear to be traveling as unit; can include foraging or exploration behaviors; responsive to the other's presence (eye/head movement as indicator); one or both members appear to be coordinating movements
<i>Neutral</i>	
Close proximity—no contact	Monkey(s) moves to <50 cm of individual(s) of other species (not simply passing to go elsewhere) but shows no interest in interacting, and does not touch
Close proximity—contact	Monkey(s) moves to <50 cm of an individual(s) of other species and makes physical contact (e.g. brushing past each other, <i>S. sciureus</i> walking under <i>S. apella</i> 's legs, touching shoulders in indoor access corridors) but shows no interest in interacting

Table 3. Definitions of the responses to, and reasons for, interspecific interactions (Leonardi et al., 2010).

Responses to interaction	Definition (recipient and actor are different species)
Vigilant—ignore	Recipient monkey(s) appears aware of behavior of the “actor” monkey(s) but does not move from area or engage with other monkey; however continued observations are made of “actor” monkey’s activities
Approach	Recipient monkey(s) moves to <50 cm of “actor” monkey
Move away	Recipient monkey(s) retreats from actor monkey and the area they were previously occupying. Includes moving short distances away (e.g. move 50 cm to next branch) or leaving enclosure
Move away then return	Recipient monkey(s) retreats from actor monkey and the area the recipient monkey was previously occupying but returns within 2 min (but often immediately)
Aggression—no contact	Recipient monkey(s) behaves in an agonistic way toward the “actor” monkey, moving into closer proximity and making threatening displays such as facial threats and vocalizations, intense rapid movements toward another individual which lead to displacement, or vigorous shaking of branches and vines. No physical contact is made
Aggression—with contact	As above but with physical contact such as grabbing, pinching, pushing, or biting
Unconcerned	Recipient monkey(s) appear aware of behavior of the “actor” monkey(s) but does not appear to be in any way adversely affected by their behavior, maintaining a relaxed position, often carrying on with previous behavior (e.g. continuing with eating or playing, and not stopping to maintain vigilance), and does not make any attempt to move away from area or actor monkey
Reasons for interactions	
Food resource	Interaction occurs around a focus of edible items; interaction may be aggressive, affiliative, or neutral
Territorial	Aggressive interactions over an area which is preferred by one species and which the other species enters, for example, a group of <i>S. sciureus</i> moving onto the branch in the <i>S. apella</i> enclosure which the <i>S. apella</i> preferentially use
Proximity	Interaction occurring involves close proximity (<50 cm)
Curious	Interaction appears to result from the interest shown by one species in member(s) of the other species. The behaviors shown are investigative, for example, sniffing or watching for extended periods of time. These are affiliative interactions; there is no competition involved and the “actor” monkey behaves in a purposeful but non-aggressive manner
Playful	Interactions are due to the energetic good-natured behavior of one or both species. This often involves affiliative interactions (e.g. eliciting play) but the occurrence of vigorous activity may also lead to an aggressive or neutral interaction (e.g. collision)
Unintended	The actions of the “actor” monkey cause an interaction without the actor showing any signs of meaning to involve the other species, for example, the actor steps on the tail of the recipient while looking in a focussed manner at something else
Accustomed (relaxed/ comfortable)	The actor monkey and/or recipient monkey(s) are at ease in the presence of the other species, that is, they either behave toward the other species in a similar way as they would toward a conspecific, or they continue behaving in the same way despite the close proximity (<50 cm) of the other species. Can involve neutral or affiliative interactions
Frustration at	The actor monkey shows signs of irritation before the recipient monkey is

another	involved, which leads to target an aggressive encounter between the two species, for example, an intraspecific aggressive encounter closely followed by an interspecific aggressive encounter
Access to area	The interaction occurs due to the actor monkey(s) attempting to move from one place to another, for example, simultaneously passing through the exit holes to the outdoor enclosure (small area)
Assert dominance	The actor monkey behaves aggressively toward the recipient monkey, using assertive postural behavior (e.g. arched back which appears to increase size, and possibly also threatening facial expression) and there are not any other factors apparent to cause the behavior (i.e. no food close by and not in a territory preferred by one species)

Table 4. The types of interactions, responses to them and the reasons for their occurrence (with frequency of occurrence). Single occasions of types of interactions are not included.

	Aggressive	Affiliative	Neutral
Type of interaction	displace non-contact (n=15) vocal exchange (n=7)	curious approach (n=12) play (n=7)	close proximity-no contact (n=29) close proximity-with contact (n=3)
2008 Phase 1			
2008 Phase 2	displace non-contact (n=4) vocal exchange(n=4)	curious approach (n=8) moving together (n=6) food beg (n=3) play (n=3)	close proximity-no contact (n=10) close proximity-with contact (n=3)
2009	chase no contact (n=13) displace non-contact (n=6) vocal exchange (n=4)	curious approach (n=9) play (n=2)	close proximity-no contact (n=10)
2010	chase contact (n=9) chase no contact (n=5) threat display (n=3)	play (n=7) curious approach (n=4)	close proximity-no contact (n=17)
Response to interaction	move away (n=16) move away then return (n=7)	approach (n=13) unconcerned (n=11)	unconcerned (n=18) vigilant ignore (n=4)
2008 Phase 1			
2008 Phase 2	move away (n=4) vocalization (n=4)	unconcerned (n=17) approach (n=5) move away then return (n=2)	unconcerned (n=13) move away then return (n=3) move away (n=2)
2009	move away (n=18) vocalization (n=3) move away then return(n=2)	move away (n=5) unconcerned (n=2) aggression-no contact (n=2) play (n=2)	move away (n=11)
2010	move away (n=11) aggression - no contact (n=3) aggression - with contact (n=2)	move away (n=7) unconcerned (n=5)	unconcerned (n=14) move away (n=4)
Reason for interaction	territorial (n=9) assert dominance (n=8) food resource (n=7)	curious (n=15) playful (n=7) food resource (n=5)	accustomed (n=12) curious (n=8)
2008 Phase 1			
2008 Phase 2	assert dominance (n=2) food resource (n=4)	curious (n=5) playful (n=5) food resource (n=7) relaxed/comfortable(n=8)	relaxed/comfortable (n=7) food resource (n=5) playful (n=4) curious (n=2)
2009	territorial (n=18) food resource (n=4)	curious (n=9) playful (n=2)	access to area (n=9)
2010	territorial (n=6) assert dominance (n=4) food resource (n=2) proximity (n=2)	curious (n=3) playful (n=7) food resource (n=3)	relaxed/comfortable (n=4) food resource (n=8) access to area (n=2) unintended (n=4)

Table 5. Direction of interspecific interactions across the years, per individual per hour (total number of interactions in brackets), with mean and standard deviation (SD)

Year	Direction	Aggressive	Affiliative	Neutral	Total
2008 Phase 1	<i>S. apella</i> to <i>S. sciureus</i>	0.037 (16)	0.042 (18)	0.054 (23)	0.133 (57)
	<i>S. sciureus</i> to <i>S. apella</i>	0.017 (17)	0.013 (13)	0.010 (10)	0.040 (40)
2008 Phase 2	<i>S. apella</i> to <i>S. sciureus</i>	0.013 (5)	0.043 (13)	0.037 (11)	0.097 (29)
	<i>S. sciureus</i> to <i>S. apella</i>	0.0064 (4)	0.019 (12)	0.014 (9)	0.039 (25)
2009	<i>S. apella</i> to <i>S. sciureus</i>	0.028 (20)	0.004 (3)	0.012 (9)	0.044 (32)
	<i>S. sciureus</i> to <i>S. apella</i>	0.003 (4)	0.007 (9)	0.002 (2)	0.012 (15)
2010	<i>S. apella</i> to <i>S. sciureus</i>	0.040 (17)	0.030 (13)	0.030 (16)	0.111 (46)
	<i>S. sciureus</i> to <i>S. apella</i>	0 (0)	0 (0)	0.004 (2)	0.004 (2)
\bar{x} +/- SD	<i>S. apella</i> to <i>S. sciureus</i>	0.030 +/-	0.039 +/-	0.033 +/-	0.034 +/-
		0.012	0.006	0.017	0.012
\bar{x} +/- SD	<i>S. sciureus</i> to <i>S. apella</i>	0.007 +/-	0.010 +/-	0.007 +/-	0.008 +/-
		0.007	0.008	0.006	0.007