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RESEARCH ARTICLE

Living Together: Behavior and Welfare in Single and Mixed Species Groups of Capuchin (*Cebus apella*) and Squirrel Monkeys (*Saimiri sciureus*)

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There are potential advantages of housing primates in mixed species exhibits for both the visiting public and the primates themselves. If the primates naturally associate in the wild, it may be more educational and enjoyable for the public to view. Increases in social complexity and stimulation may be enriching for the primates. However, mixed species exhibits might also create welfare problems such as stress from interspecific aggression. We present data on the behavior of single and mixed species groups of capuchin monkeys (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*) housed at the Living Links to Human Evolution Research Centre in the Royal Zoological Society of Scotland's Edinburgh Zoo. These species associate in the wild, gaining foraging benefits and decreased predation. But *Cebus* are also predators themselves with potential risks for the smaller *Saimiri*. To study their living together we took scan samples at ≥ 15 min intervals on single ($n = 109$) and mixed species groups ($n = 152$), and all occurrences of intraspecific aggression and interspecific interactions were recorded. We found no evidence of chronic stress and *Saimiri* actively chose to associate with *Cebus*. On 79% of scans, the two species simultaneously occupied the same part of their enclosure. No vertical displacement was observed. Interspecific interactions were common (>2.5/hr), and equally divided among mildly aggressive, neutral, and affiliative interactions such as play. Only one aggressive interaction involved physical contact and was non-injurious. Aggressive interactions were mostly (65%) displacements and vocal exchanges, initiated almost equally by *Cebus* and *Saimiri*. Modifications to the enclosure were successful in reducing these mildly aggressive interactions with affiliative interactions increasing in frequency and diversity. Our data suggest that in carefully designed, large enclosures, naturally associating monkeys are able to live harmoniously and are enriched by each other. Am. J. Primatol. 72:33–47, 2010.

Key words: mixed species zoo exhibit; social enrichment; welfare; *Cebus*; *Saimiri*

INTRODUCTION

Although efforts are commonly made to provide environmental enrichment for captive primates, social enrichment is relatively neglected, as it is rarely straightforward or risk-free [Visalberghi & Anderson, 1993]. Housing different species together may be one way to enrich them socially, and can be beneficial for zoos where each species is below natural group sizes. One potential advantage lies in the increases in activity found in mixed species troops [e.g. Buchanan-Smith, 1999; Hardie, 1997; Heymann et al., 1996]. Such increases in activity may reflect higher levels of both physical and psychological stimulation, enhancing primates' well-being [Thomas and Maruska, 1996]. Mixed species troops may also benefit from being housed in a bigger enclosure [Baker, 1992; Hardie et al., 1993; Xanten, 1990, 1992]. For species that associate together in the wild, social complexities in mixed species enclosures should provide a more natural life. Increasing efforts are focused on creating captive environments that facilitate natural behaviors [Hosey, 2005], for which appropriate social environments may be critical. Displaying animals in their appropriate social context should also allow the viewing public to gain greater understanding of the species' natural environment, and observing interspecific interactions may create a more interesting

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and enjoyable viewing experience [Dalton & Buchanan-Smith, 2005; Hardie et al., 2003; Xanten, 1992].

Despite such potential benefits, mixed species exhibits have varying degrees of success. A review by Sodaro [1999] emphasizes that the successful formation of a mixed species troop does not guarantee long term advantages. Sodaro notes that in comparison with traditional housing of single species groups of primates, mixed species troops may require higher levels of monitoring to ensure welfare is not compromised.

Although there are many factors contributing to how successful the captive primate mixed species troops will be, a key consideration is whether they would actively form associations in the wild [Hardie et al., 2003]. The primate species involved in this present study, capuchin (*Cebus apella*) and squirrel (*Saimiri sciureus*) monkeys, actively associate in their natural environments, forming temporary but stable mixed species troops for over 50% of their time, with associations lasting from a few hours to 12 days [Podolsky, 1990]. *C. apella* is the most widely distributed of the capuchin species [Fragaszy et al., 2004], found across much of northern and central South America (Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, French Guiana, Suriname, and Guyana). It is sympatric over many of these areas with *S. sciureus*, although *S. sciureus* is absent from the eastern Brazilian coastal forests [Baldwin & Baldwin, 1981].

Of the primate species known to associate, these two species have the greatest relative difference in body size; *C. apella* is considerably larger than *S. sciureus*; with adult males typically weighing an average of 3 kg, compared with 0.74 kg, respectively [Jack, 2007]. Although reports of group sizes vary between study sites, the mean group size of *C. apella* is 17 individuals (averaged from various field sites [Fragaszy et al., 2004]), with a typical mixed-sex composition including one alpha male, multiple subordinate adult males and adult females, and assorted subadults, juveniles and infants. Troops of *S. sciureus* typically range between 30 and 70 individuals, and are again of multi-male, multi-female composition [Mitchell, 1994; Terborgh, 1983] although Boinski et al. [2003] report a low mean group size of 23. The intermittent nature of the interspecific association is thought to arise from differences in food requirements that lead to differing ranging habits; the ranges of *S. sciureus* are far more extensive than their larger associates [Terborgh, 1983]. Further niche differentiation arises because *C. apella* are more frugivorous, and *S. sciureus* relatively more insectivorous. *Cebus* are more likely to be found in the middle canopy, moving quadrupedally on medium-sized support branches, whereas the *Saimiri* are more saltatory, and move on the smallest of arboreal supports [Fleagle et al., 1981].

Examining the reasons for the high level of association between *C. apella* and *S. sciureus,* Terborgh [1983] concluded that the *Saimiri* played an active part in initiating, maintaining, and dissolving the associations, while the behavior of the *Cebus* troops was less likely to be affected by the *Saimiri's* movements. Terborgh [1983] concluded that the *Saimiri* benefit from the *Cebus'* more detailed knowledge of fruiting trees, as their associations with *Cebus* increased during periods of resource scarcity, and *Cebus* led the troop more frequently during periods of rapid travel (leading to either fruiting trees or new foraging areas). However, as associations continued in periods when resources were at their most abundant Terborgh [1983] suggested that it is instead the superior predator alarms emitted by the vigilant male *Cebus* which is the greatest benefit to *Saimiri* who respond more readily to *Cebus* alarm calls than they do to the alarm calls made by their own species. *Saimiri* calls typically serve to maintain contact between group members, rather than directly functioning in predator avoidance or detection [Jack, 2007]. In a recent experimental field study, Stone [2007] found that the adult *S. sciureus* foraged intensively and did not behave in a predator sensitive manner, regardless of the seasonal abundance of food, whereas the juveniles (who are particularly vulnerable to predator attacks) adjusted their feeding behavior according to the concealment that particular areas offered from predators. The existence of shared predators suggests that *Cebus* may also benefit from a diluted predation risk in larger mixed species groups, particularly as *Cebus* are the larger species and tend to be located centrally within the mixed species troop (the selfish herd effect [Terborgh, 1983]). Yet considering the little attention that the *Cebus* pay to the *Saimiri's* behavior or calls, and the increased distance (approximately 40% further) that the *Cebus* troops travel when in association, Terborgh [1983] concludes that the *Cebus* receive fewer benefits from the association, and overall the effect of the presence of *Saimiri* is neutral or slightly negative. In contrast to this conclusion, Podolsky [1990] who like Terborgh also studied single and mixed species troops *of Cebus* and *Saimiri* at Manu, Peru, found several benefits to *Cebus* associating with *Saimiri*. Although both species increased their consumption of fruit and nectar when in association, the particular effects varied for each species. *Cebus* were again found to lead *Saimiri* to the larger fruiting trees, they controlled access to the best feeding sites, and their feeding rates increased when *Saimiri* were present at the same fruiting tree, whereas the *Saimiri* feeding rates declined (although the proportion of large fruiting trees visited by *Saimiri* was more when in association). When in association, *Cebus* also benefited from searching over a wider area (twice the swathe in association than alone) and by monopolizing smaller fruiting resources located by *Saimiri* [Podolsky, 1990]. The higher feeding rates of individual *Cebus* when feeding in close proximity to *Saimiri* were due to their decreased vigilance in the larger mixed species group [Podolsky, 1985 cited in Podolsky, 1990]. This suggests that *Cebus* also gain benefits related to reduced predation threats when in association [Podolsky, 1990].

In view of their association in their natural habitat, there might be both benefits and costs of forming mixed species groups of *C. apella* and *S. sciureus* in captivity. Each species may benefit from a more natural social environment, with increased social stimulation and the additional advantage of a larger enclosure. Such benefits would surely have a positive effect on the primates' welfare. However, there are also welfare concerns that must be taken into account. Associations in the wild are temporary, allowing either species to return to a single species troop; choices to do so may be more limited in captivity. As individual *Cebus* typically displace the smaller *Saimiri* from the best feeding sites, this raises concerns for the smaller species' access to resources in a competitive and restricted environment. In addition, the presence of a larger dominant species might act as a stressor when in a captive situation; conversely, the presence of a larger and exceedingly active group of *Saimiri* might have a negative impact on the quieter *Cebus* group. Although the agonistic interactions reported by Podolsky [1990] show non-contact threats and displacements to be common at feeding sites in the wild, there is a possibility that there would be reduced tolerance and increased risk of physical harm in a restricted captive environment.

However, there is one anecdotal report of a successful, long established trispecific group of *C. apella, S. sciureus* and *Ateles geoffroyi* at Chicago Zoological Park [Sodaro, 1999]. The group composed of 14 *Cebus* and up to 22 *Saimiri* of varied age/sex composition, and no negative interactions between these two species were observed (although there were occasional negative interactions between each species and individual *Ateles*). Close relationships were observed between several of the juvenile *Cebus* and *Saimiri,* with positive interactions including both species engaging in play behaviors, and the *Saimiri* sitting in the ''laps'' of juvenile *Cebus* females. Even when placed in a smaller area (in linked holding cages during enclosure renovations) the two species mingled freely without any interspecific aggression being observed; the two most subordinate *C. apella* females chose to occupy cages with the *S. sciureus*. There are also numerous reports of other primate species being successfully maintained in mixed species groups in captivity [e.g. Hardie, 1997; Hardie et al., 2003; Heymann et al., 1996; Sodaro, 1999; Xanten, 1990], with varying degrees of success. When manipulating the social environment of primate species in captivity, risks can be minimized by a good knowledge of the species' normal behaviors, and by continued careful monitoring [Visalberghi & Anderson, 1993]. Different methods of interspecies introductions, sufficient planning of the captive environment and extensive preparations for the integration of the two species into their new environment are proposed as ways to maximize the chances that the mixed species combinations will succeed [Sodaro, 1999]. While combinations of *Saimiri* with *Cebus* may be a potentially successful proposition, there have been very few attempts to house them together in captivity. In addition, there have been no systematic observations of such mixed species groups.

The aim of this study was to assess the behavior and welfare of *C. apella* and *S. sciureus* in single and mixed species groups. By recording each individual's activity and location in the same environment in both single and mixed species groups, it is possible to assess potential negative or positive effects of the presence of the other species. The focus of our study is on behaviors that may be indicative of welfare. For example, reductions in the frequency of positive or affiliative behaviors such as play and grooming could raise concerns for the primates' well-being [Burghardt, 2005; JWGR, 2009]; conversely significant increases in agitated behaviors such as scratching or fast locomotion can be representative of increased levels of anxiety or stress [Aureli & Schaffner, 2002; Badihi, 2006; Maestripieri et al., 1992] and increases in intraspecific aggression would also be of concern [JWGR, 2009]. By examining the differences in the enclosure use (indoor/outdoor, height, location, and substrate) as well as behavior in both single and mixed species groups, it is possible to assess if either species avoids or is deterred from particular areas by the other species; alternatively, this information may reveal if the *Saimiri* or *Cebus* are attracted to associate with the other species. In addition, by recording the interspecific interactions between the two species, the social dynamics of such mixed species groups is better understood. By assessing these interactions, it will be possible to determine if the levels of aggression between the two species are a cause for concern in a restricted captive environment. However, as there have been reports of affiliative interspecific relationships in a similar mixed species group in captivity, positive interactions between individuals are also of interest, to determine the potentially socially enriching effects of mixed species groups.

Based on the descriptions of the association between *C. apella* and *S. sciureus* in their natural habitat [Podolsky, 1990; Terborgh, 1983] and of an anecdotal report of an established mixed species group in captivity [Sodaro, 1999], we expect

1. *Saimiri* to be the initiators of associations between the two species, and to use the outdoor enclosure (where perceived predation risk is likely

to be higher than indoors) more when in mixed species groups.
2. *Cebus* to be the dominant species, and for this to adversely affect *Saimiri's* use of the enclosure when the *Cebus* are present.
3. Interspecific interactions to occur and for *Cebus* to be dominant in these encounters. It is also predicted that more affiliative interspecific interactions will occur between youngsters.

METHODS

Housing and Husbandry

Two mixed species groups of common squirrel monkey (*S. sciureus)* and brown capuchin (*C. apella)* were formed in May 2008 at the Living Links to Human Evolution Research Centre, situated within the Royal Zoological Society of Scotland (Edinburgh Zoo, see http://www.living-links.org/). This facility was designed as a research centre and a ''public engagement with science'' exhibit. Enclosures for the two mixed species groups mirror each other on either side of a central visitors' viewing platform, and are named the ''West'' and ''East'' wings (Fig. 1). Each wing includes an indoor *Saimiri* enclosure (5.5 m × 4.5 m × 6 m high), to which only the *Saimiri* are small enough to gain access, an indoor *Cebus* enclosure (7 m × 4.5 m × 6 m high) in which both the species are able to enter, and a large shared outdoor enclosure (approximately 900 m^2). A research room with testing cubicles is situated between the indoor enclosures in each wing, and a holding room is present adjacent to each indoor enclosure should separation of the monkeys be required (e.g. for veterinary treatment). Temperatures in the indoor enclosures are approximately 24°C, maintained using radiant ceiling heaters and the air conditioning system, and artificial lights are on a 12 hr cycle, 7.30–19.30 hr, controlled by digital timers. There is also considerable natural light in the enclosures; each enclosure has four windows. There are also sun chimneys in the ceiling. All indoor enclosures have a bio-floor surface, covered in bark chips, and a minimum of five trees (some living) that support a network of branches. Artificial rock areas are located in the rear walls and corners of the enclosures (from ground level to ~4 m in height), and wooden feeding platforms (0.3 × 0.5 m^2) are fixed to suitable trees. Further networks are provided by lengths of liana and artificial vines that are distributed throughout both the indoor and outdoor enclosures.

Each indoor enclosure has three exit/entrance routes from to the outdoor enclosure; one leads directly out, one passes through the holding cages, and another runs through the training cubicles in the research rooms (Fig. 1). The ground substrates of the outdoor enclosures consist of a mixture of bark chip, grass and dry river bed/soil areas; each enclosure contains 18 trees, with networks of branches, sections of liana and rubber vines connecting them. As the outdoor enclosures have no roof, trees are located centrally in the enclosure (to allow for a possible 7 m jump zone). Perimeter mesh fences are 2.4 m high, with electric hot wires at the top. Many small bushes and large boulders are distributed toward the boundaries of the outdoor

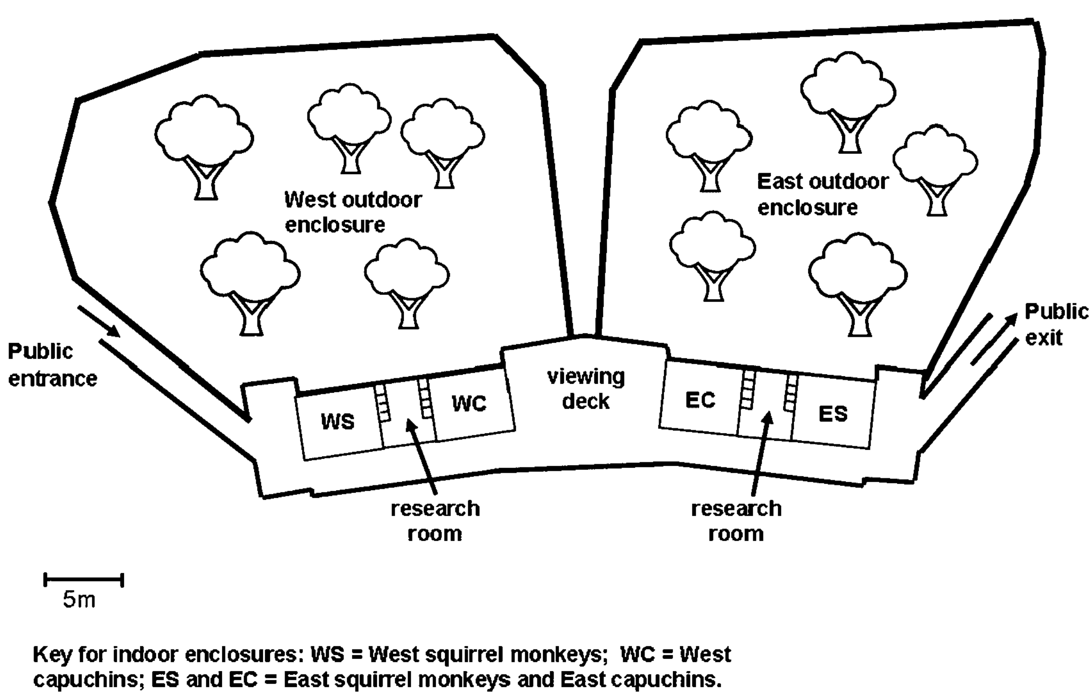

Fig. 1. Schematic diagram of the Living Links to Human Evolution Research Centre, approximately to scale.

enclosures, and 14 dead trees are laid at ground level to increase low level networks and provide easy access to scattered food. Both species are allowed free access between indoor and outdoor enclosures, except during routine husbandry and by request of researchers, as in the course of this study. While no monkey has been preyed upon, raptors and crows are regularly present in the outdoor enclosures and are treated by the primates as perceived threats.

Daily routines typically include a main morning and a main afternoon feed, and three to four scatter feeds distributed throughout the remainder of the day. All the indoor enclosure windows are thoroughly cleaned each morning and branches once weekly, once, with cleaning and maintenance in the outdoor enclosures as needed. The diets for the two species are similar (with amounts given, size of items and frequency of feeding of particular foods differing slightly between the two species), and consist of a wide variety of fresh fruits, vegetables, primate pellets, hard-boiled eggs, chicken, insects, and larvae (mealworms, locusts, crickets, etc., typically twice daily for *Saimiri* in scatter feeds and at least twice a week for *Cebus*) and vitamin supplements (sprinkled on feed). Scatter feeds also include mixed seeds, nuts, raisins, and dates. Dried fruits and nuts that are preferred are also used in training sessions by keepers (e.g. positive reinforcement training for husbandry). Water is constantly available in automatic drinkers in the indoor enclosures and holding cages.

Subjects

At the beginning of observations, the West *Cebus* group was composed of 3 adult females (13, 6, and 5 years), 2 young males (4 and 2 years), 1 male infant (5 months) and 1 very young infant *Cebus* who remained on his mother's back and was not included in scans, but was included for interactions (see below). The West *Saimiri* group was composed of 15 individuals; 1 adult male (alpha, 8 years), 3 young males, and 1 young female (all 2 years), 7 adult females (4–9 years) and 3 male infants (7 months). The East *Cebus* group consisted of 5 individuals; one ~37 years wild caught adult (alpha) male, 3 younger males (2–7 years), and one adult female (6 years). The East *Saimiri* group consisted of 1 subadult male (despite his young age, as the oldest male in the troop, this male was alpha and sexually active at 3 years), 6 adult females (3–7 years), and 3 infants (2 male and 1 female, all approx. 7 months). Individuals were categorized as youngsters at <4 years in *Cebus* and <2 years in *Saimiri*. The *Cebus* were distinctive enough to be identified individually without artificial aid whereas the majority of *Saimiri* wore ball chain collars with color coded beads.

Both species were given time to adjust in the indoor enclosures following the move to the facility, before being introduced to the outdoor enclosures and being mixed; all members had previously been housed in single species groups. For the East group, both the *Cebus* and *Saimiri* groups were given access to the outdoor enclosures in single species conditions, to allow them to familiarize themselves with the enclosures, before being given mutual outdoor access in a mixed species situation. The mixing procedure for the West group, although intended to be the same, was slightly different; there were initially concerns that the very young baby *Saimiri* in this group may be at risk from natural predators, and so the *Cebus* were first given access outside while the *Saimiri* group were also outside, as the *Cebus* presence had previously been found to deter such predators. Events during the initial mixing period (May 2008) were monitored by the resident researcher and keepers. The mixing was successful, with no incidents between the two species causing concern. The large and complex enclosures offering space, visual barriers and escape routes were thought to be critical in the successful formation of the mixed species groups, although the West *Cebus* group were nervous to explore their new enclosures in the absence of an alpha male (who was removed from this family group before the move, for husbandry purposes).

Phase 1: Behavior and Welfare in Single and Mixed Species Groups

Rationale

To determine how each species was affected by living in mixed species groups, in Phase 1 we examined the behavior and location of each species, observing the groups in both single and mixed species conditions. We recorded interspecific interactions and intraspecific aggressions to assess any welfare concerns.

Procedure

Data collection was carried out in July and August 2008 by R. L. We used scan sampling methods [Martin & Bateson, 2007] to record the behavior, enclosure, substrate, and height occupied for each individual, sampling both species in the mixed groups concurrently. We collected scans of all group members at a minimum of 15 min intervals. We recorded each individual in the inside enclosures first, choosing individuals from left to right, then individuals in the outdoor enclosure and finally any individuals who had not been recorded. Once an individual was located and identified, the observer counted 5 sec and then recorded the individual at that exact time point of 5 sec to avoid over sampling conspicuous behaviors. Recording took place between 08.30 and 18.00 hr, with a similar number of scans in each hourly period. We accumulated a total of 152 scans in mixed, and 109 in single species groups. Scans were distributed over different periods of the day as a whole, with occasional longer intervals between scans (e.g. due to husbandry practices).

In addition to scan sampling, we used ad libitum sampling to record all occurrences of interspecific interactions and intraspecific aggression using a set format recorded directly to Dictaphone. We calculated the total durations of time spent observing each day (for single and mixed conditions), to give rates per hour of such behaviors. These rates 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. When recording inter and intraspecific interactions, we noted the details of the event, the type of interaction, along with the direction of the interaction, the response to it, and the individuals involved. We defined behaviors unambiguously following pilot work [with reference to Baldwin & Baldwin, 1981; Freese & Oppenheimer, 1981; see Tables I–IV for those relevant to this study]. We coded locations and substrates, and categorized heights occupied as ground level, <2, 2–4, and >4 m. Due to occasions when individuals could not be recorded during scans (e.g. individuals were in the holding cage area, which was not visible) we transformed data from the scans to percentages, to allow for an accurate description of the activities and locations of the group. All *Cebus* were recorded on scans but on average 8% of *Saimiri* were out of sight on scans.

For single species conditions, one species was kept in their indoor enclosure (from the previous evening on all cases except one, in which *Cebus* were contained early on the morning of observations), allowing the species that was being observed to have full use of their indoor enclosure and the outdoor enclosure for the following days. We did not collect data on mixed species on the same day on which re-mixing occurred, as location and behaviors may have been affected. Data collection methods in single and mixed species groups were identical. We collected single species data on the East *Saimiri* and *Cebus* groups, and for the West *Cebus* group, but not the West *Saimiri*, as the West *Cebus* group were slow to gain confidence to use the outdoor enclosure, so it was considered better not to restrict their access outside at the time of data collection. As the two *Cebus* groups showed marked differences in group composition, activity, and enclosure use, we analyzed all the data separately for West and East groups, and separately by species. The total scan numbers for East and West in mixed species was 38; in single species were 31 scans for East *Saimiri*, 38 for East *Cebus*, and 40 for West *Cebus* (no single species data were collected for West *Saimiri*).

Phase 2: Behavior and Welfare in Mixed Species Groups Following Enclosure Refurbishment

Rationale

The data from Phase 1 suggested that enclosure changes were likely to have a positive effect on the interactions observed between the two species, and on the behavior and welfare of the animals. In Phase 2 we recorded behavior following enclosure refurbishment.

Procedure

We made changes to the enclosures that were designed to increase their use, improve resting/sleeping areas, reduce competition over preferred areas, improve escape routes, and increase feed sites. Such changes included adding new branches to increase the networks and connections between branches and trees, providing wider horizontal branches to increase the number of sleep sites (nocturnal CCTV footage showed these to be limited), adding woven swinging baskets (that both

TABLE I. Definitions of Behaviors Used in Scan Sampling

Welfare indicators	Definition
Play and play elicitation	Monkey engages in high activity interaction (e.g. chase, rough and tumble, mock wrestling) with other individuals. This can include nonaggressive physical contact, or occur at a distance, for example, hopping and running, steep leaps (almost vertical jumps with minimal forward locomotion) or swinging by the feet, while visually checking/coordinating with play partners. Behaviors that are used to elicit play are also included, for example, looking through legs or rolling/lolling on back while looking at potential play partner
Allogroom	The monkey's hands and/or lips are drawn through the coat, skin, or teeth of another and particles are occasionally removed
Fast locomotion	Monkey is moving in relation to its surroundings: movements are made at a rapid pace, that is, running speed and also include jumping and leaping when there is more than one leap/jump made, that is, a succession. Is not scored when playing
Intraspecific aggression	A monkey is involved in an agonistic conflict with one or more other monkeys, either as the initiator or in defence. This can include facial threats, for example, retracted lips (with mouth open in *Cebus*), grimaces and/or vocalizations (e.g. shrieks or screams), intense rapid movements toward another individual that lead to displacement, vigorous shaking of branches and vines or threatening physical contact such as grasping, slapping, pulling, biting, or jumping onto

TABLE II. Definitions of Types of Interspecific Interactions Broken Down by Category

Interaction type	Definition
Aggressive	
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 (*Saimiri*), facial grimaces (retracted lips, mouth open in *Cebus*), branch shaking, or rapid body movements in their direction (thrusting head forward then pulling back). No physical contact is made
Affiliative	
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 (see Table I). Also includes attempts to join in intraspecific play, for example, moving close and engaging in similar play behaviors
Food share passive	The possessor of the edible item neither solicits nor resists the attempts of member(s) of the other species to take it [after Hoage, 1982]. Individuals remain in close proximity to each other and do not engage in aggressive 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 (<2 m) 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 co-ordinating movements
Neutral	
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, *Saimiri* walking under *Cebus*' legs, touching shoulders in indoor access corridors) but shows no interest in interacting
Unclear	An interaction occurs between two or more monkeys of different species, but it is difficult to discern the type of interaction (e.g. many members, or many overlapping types of interaction occurring at once, making it difficult to establish overriding type)

species liked to play in), and adding new feeding stations. We then resumed data collection on mixed species groups to assess whether the changes had any effect on the animals' behavior and use of the enclosures. We collected data using the same methods as in Phase 1 (no. of mixed species scans = 57). Data were tested for normality and analyzed using parametric statistics. In none of the statistical analyses done was Bonferroni correction carried out as although they reduce the probability of Type I error, at the same time they increase the probability of Type II error (Caldwell et al., 2005). One of the three behaviors analyzed by *t*-tests and ANOVAs on each group produced a potentially spurious result in one group (possibly Type I), but all others were in a consistent pattern to that predicted. The research was approved by the University of Stirling Psychology Department Ethics Committee and adhered to the legal requirements in the United Kingdom.

RESULTS

Phase 1: Behavior and Welfare in Single and Mixed Species Groups

Enclosure use

In order to assess the effects that being in mixed species groups had upon the monkeys' use of the enclosures, we compared the mean percentage of each species occupying each enclosure (indoor/outdoor) in single and in mixed species conditions. If the larger group size in mixed species confers increased confidence, we might expect there to be a greater proportion of each species outside in mixed species conditions. However, if the presence of the other species is threatening or stressful, we might expect

TABLE III. Definitions of Responses to Interspecific Interactions

Responses to interactions	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
Vocalization	Recipient monkey(s) faces the "actor" monkey(s) and makes a call, for example, shrieks or screams
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)
Segregate into species groups	Members of the two species move toward their own species members to form a cluster, having previously been mixed in enclosure. This is typically followed by the species groups facing each other and vocalizing until one species group moves away
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	Recipient monkey(s) behaves in an agonistic way toward the "actor" monkey, moving into closer proximity and making threatening movements (as described above) but making physical contact such as grabbing, pinching, pushing, or biting
Unaware—no reaction	Recipient monkey(s) does not respond to the behavior of the "actor" monkey(s), for example, does not look in direction of "actor" monkey or respond in any way
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

more of the group to remain in the safety of their indoor enclosure when in mixed species conditions.

In single species, the mean percentage of the West *Cebus* group in the indoor enclosure was 86, with a mean of 14% in the outdoor enclosure. We did not collect data for single species in the West *Saimiri* group (as we decided not to restrict outside access for the West *Cebus* group). The mean percentage of the *Cebus* group in each enclosure was very similar between mixed species groups (87% indoor; 13% outdoor) and single species groups and did not differ significantly ($t(76) = -0.082$, $P = 0.935$). The mean percentage of the *Saimiri* group in their own enclosure was 47, with 23% in the outdoor enclosure and 23% occupying the *Cebus* enclosure (mean of 7% out of sight).

The East *Cebus* group behaved quite differently to the West *Cebus* group. In a single species, the mean percentage of the group in the indoor enclosure was 10, with a mean of 90% in the outdoor enclosure. The East *Saimiri* group divided their time equally between the indoor and outdoor enclosure (46% in each) when in single species groups (and 8% out of sight). When in mixed species groups, the percentage of *Cebus* in the indoor enclosure increased significantly to 28; and conversely decreased outside to 72 ($t(64.5) = 2.73$, $P < 0.01$). The mean percentage of the *Saimiri* group in their own enclosure reduced to 43, with 34% in the outdoor enclosure, 13% of the group occupying the *Cebus* indoor enclosure and 10% out of sight. However, these changes in enclosure use were not significant for *Saimiri* ($P > 0.05$).

In addition to examining enclosure use in mixed species groups, we were also interested in how much time the two species chose to spend in the same enclosure. For both West and East groups, the percentage of scans in which the two species were co-present in the same enclosure was identical at 79% ($n = 78$ in both West and East). In addition, when in mixed species conditions the West *Cebus* group never went outside without members of the West *Saimiri* group being present. Conversely, the East *Saimiri* group never went outside without members of the East *Cebus* group being present.

Heights occupied in enclosures

If competition between the two species affect their use of the enclosure, vertical displacement may be expected. The mean percentage of *Cebus* at each height level is distinctly different between the West and East groups, with the majority of the West group occupying heights of >4m in their enclosures, while the East *Cebus* group are more evenly distributed between the different height levels in the enclosures (Fig. 2). Both West and East *Saimiri* groups distribute themselves across the vertical dimension, but are rarely on the ground. The mean percentage of each species occupying each height level are very similar in single and mixed species conditions; independent samples *t*-tests revealed no significant

TABLE IV. Definitions of Reasons for Interspecific Interactions

Reasons for interactions	Definitions
Food resource	Interspecific interaction occurs around a focus of edible items; interaction may be aggressive, affiliative, or neutral
Territorial	Interspecific aggressive interactions over an area which is preferred by one species and which the other species enters, for example, a group of *Saimiri* moving onto the branch in the *Cebus'* enclosure which the *Cebus* preferentially use
Proximity	Interspecific interaction occurring involves close proximity (<50 cm)
Protective	The interspecific interaction initially occurs and another member of the recipient's species becomes involved in a defensive manner, for example, mother becomes aggressively involved in an interaction involving her offspring
Curiosity	Interaction between the two species 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 nonaggressive 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 another target	The actor monkey shows signs of irritation before the recipient monkey is involved, which leads to 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)

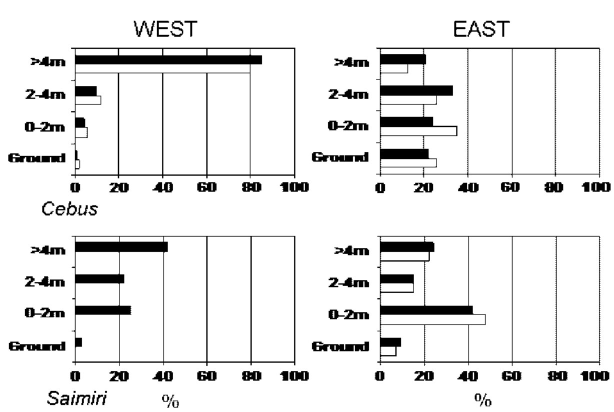

Fig. 2. Percentage of monkeys at each height in single (light bars) and mixed species (dark bars) groups.

differences in height distribution between single and mixed species conditions ($P>0.05$ for all).

Behavior: welfare indicators

We examined allogrooming (*Cebus* only), fast locomotion and play as possible welfare indicators, comparing the mean percentage of each group engaging in these behaviors in a single and mixed species conditions to determine if the association had any negative effects on the monkeys' behavior (Table V). Allogrooming categories were collapsed to include both being groomed and grooming another.

One-way ANOVAs indicated no significant differences in the percentage of both West and East *Cebus* groups engaging in allogrooming, fast locomotion, or play behaviors in a single and mixed species conditions (Table V). Similarly, no significant differences were found in the percentage of the East *Saimiri* group engaging in fast locomotion or play behaviors in a single and mixed species conditions.

Frequencies of Intraspecific Aggression

All occurrences of intraspecific aggression were recorded in both single and mixed species groups. In 36 hr of single species observations, 17 occurrences of intraspecific aggression were recorded, giving a rate of 0.5/hr (two single species *Cebus* conditions and one single species *Saimiri*). However, in mixed species conditions the frequency of intraspecific aggression

TABLE V. Mean % of Individuals in *Cebus* and *Saimiri* Groups Engaging in Behaviors When in Single and Mixed Species Conditions

	West		East	
	Mean (SD)	ANOVA result	Mean (SD)	ANOVA result
Cebus				
Allogroom				
Single species	9 (16)	$F(1, 76) = 0.15, P>0.05$	3 (9)	$F(1, 74) = 1.12, P>0.05$
Mixed species	8 (12)		5 (12)	
Fast locomotion				
Single species	6 (10)	$F(1, 76) = 1.40, P>0.05$	3 (7)	$F(1, 74) = 0.63, P>0.05$
Mixed species	4 (7)		5 (10)	
Play				
Single species	3 (8)	$F(1, 76) = 2.84, P>0.05$	14 (20)	$F(1, 74) = 0.00, P>0.05$
Mixed species	7 (15)		14 (22)	
Saimiri				
Fast locomotion				
Single species	N/A	N/A	3 (6)	$F(1, 67) = 2.60, P>0.05$
Mixed species	6 (6)	N/A	6 (11)	
Play				
Single species	N/A	N/A	4 (8)	$F(1, 67) = 0.85, P>0.05$
Mixed species	8 (9)	N/A	6 (9)	

TABLE VI. Frequency of Directions of Interspecific Interactions

Direction	Aggressive	Affiliative	Neutral	Total
Cebus to *Saimiri*	14	10	13	37
Cebus to *Saimiri* then reversed	2	8	10	20
Saimiri to *Cebus*	13	4	4	21
Saimiri to *Cebus* then reversed	4	9	6	19

was less; in 39 hr of mixed species observations, 11 occurrences of aggression were recorded, a rate of 0.3/hr. This effect was particularly pronounced in the *Cebus* groups, for whom the rate of intraspecific aggression decreased threefold when in mixed species conditions (single species = 0.33/hr, mixed species = 0.1/hr).

Interspecific Interactions

In 39 hr of mixed species observations of the West and East groups, 98 interspecific interactions were recorded, a rate of 2.5 interactions/hr. The interactions observed were found to be evenly distributed between the interaction categories; 35% aggressive ($n = 34$), 31% affiliative ($n = 31$), and 34% of neutral interactions ($n = 33$).

The most common type of aggressive interaction observed was "displace non-contact" ($n = 15$), followed by "vocal exchange" ($n = 7$). Only one aggressive interaction involved physical contact, as an adult female *Cebus* attempted to displace a young *Saimiri*. This did not result in injury. The most frequent response to aggression was to "move away" ($n = 16$), followed by "move away and then return" ($n = 7$). The types of affiliative interaction which were observed most frequently were "curious approach" ($n = 12$) and "play" ($n = 7$). The most frequent response to the affiliative interactions was to "approach" the actor ($n = 13$), followed by being "unconcerned" ($n = 11$). The neutral interaction types that were most frequently observed were "close proximity no contact" ($n = 29$) and "close proximity with contact" ($n = 3$). The most frequent response to the neutral interactions was to be "unconcerned" ($n = 18$), followed by "vigilant-ignore" ($n = 4$).

West and East groups were similar in the frequency of aggressive (West = 16, East = 18) and neutral interactions (West = 17, East = 16). However, a significantly greater number of affiliative interactions were observed in the West group ($n = 22$) in comparison with the East group ($n = 9$) (binomial, $P < 0.01$). There were more youngsters in the West group that may explain this finding (see below).

The direction of aggressive interactions was very similar for both species (Table VI). *Cebus* initiated affiliative interactions more frequently, although both *Cebus* and *Saimiri* were relatively similar in interacting in an affiliative manner when the interaction was instigated by the other species. The neutral interactions were directed most frequently from *Cebus* to *Saimiri*.

The most common reason for aggressive interactions was ''territorial'' ($n = 9$), followed by ''assert dominance'' ($n = 8$) then ''food resource'' ($n = 7$). The most frequent reason for the affiliative interactions was ''curiosity'' ($n = 15$), followed by ''playfulness'' ($n = 7$) and ''food resource'' ($n = 5$). The most frequent neutral interactions were due to the monkeys being ''accustomed'' to the other species ($n = 12$) and ''curious'' ($n = 8$).

In a total across the West and East groups, there were 16 youngsters (43%) and 21 adults (57%). Of the 31 affiliative interactions in which a main actor was identified, significantly more were initiated by youngsters than adults (74%, binomial, $P < 0.01$). Youngsters were not more likely to be the main recipients (53%, binomial, $P > 0.05$). Similarly for neutral interactions ($n = 25$), 60% of the main actors were youngsters, significantly more than expected (binomial, $P < 0.05$). The main actors in aggressive interactions were similar to the expected distributions (40% by youngsters, $n = 28$, $P > 0.05$).

Phase 2: Behavior and Welfare in Mixed Species Groups Following Enclosure Refurbishment

In order to assess the effects of the enclosure changes we compared data collected in Phase 2 of the study with the data collected in Phase 1. One-way ANOVAs revealed no significant differences between Phase 1 and 2 in play (West *Cebus* $F(1, 105) = 2.61$; East *Cebus*, $F(1, 102) = 0.001$; West *Saimiri*, $F(1, 65) = 2.09$, $P > 0.05$) or allogroom behaviors (West *Cebus* $F(1, 105) = 0.79$; East *Cebus* $F(1, 102) = 1.28$, $Ps > 0.05$). A marginally significant reduction was found in the percentage of the East *Saimiri* group engaging in play (Phase 1 mean = 4.6%, Phase 2 = 1.1%, $F(1, 95) = 4.16$, $P = 0.044$) that may be a Type I error from multiple analyses as it does not fit the otherwise consistent pattern of findings. There was a significant reduction in the percentage of the West *Cebus* group engaging in fast locomotion following enclosure refurbishment (5.1% in Phase 1; 1.2% in Phase 2, $F(1, 105) = 5.63$, $P = 0.019$). A similar significant reduction in fast locomotion was found for the East *Cebus* group (4.0% in Phase 1; 0% in Phase 2, $F(1, 102) = 5.79$, $P = 0.018$). No significant differences were found for the percentage of the West or East *Saimiri* group engaging in fast locomotion (respectively, $F(1, 65) = 3.08$, and $F(1, 95) = 2.27$, $Ps > 0.05$).

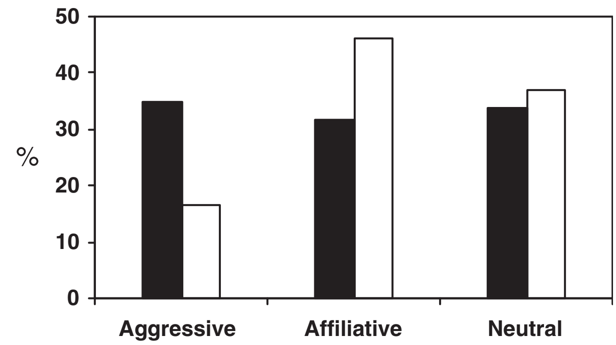

Fig. 3. Percentage of interaction types: Phase 1 (dark bars, $n = 98$ in 39 hr observation) and Phase 2 (light bars, $n = 54$ in 25 hr).

Interspecific interactions

The frequencies of aggressive, affiliative, and neutral interactions in Phase 1 and Phase 2 of observations are shown in Fig. 3. The rate of interactions in Phase 2 (54 in 25 hr, 2.2/hr) was similar to Phase 1 (2.5/hr). The proportion of affiliative interactions increased, while the aggressive interactions decreased significantly ($\chi^2 = 6.1$, df = 2, $P < 0.05$). The types of aggression that occurred continued to be mild forms, with the most common being ''displace—no contact'' ($n = 4$) and ''vocal exchange'' ($n = 4$). The most frequent forms of affiliative interaction that occurred were ''curious approach'' ($n = 8$), ''moving together'' ($n = 6$); ''close proximity—no contact'' remained the most common type of neutral interaction ($n = 10$). The rate/hr of mixed species intraspecific aggression was 0.24/hr (0.3/hr in Phase 1).

DISCUSSION

Although efforts are increasingly made to enrich environments and encourage natural behaviors of primates in captivity, primate species are typically housed in single species groups, even if the species typically form mixed species associations in the wild. As *C. apella* and *S. sciureus* actively form mixed species groups in their natural habitat, creating a captive environment which allows for similar associations, has many potential benefits. However, this option may often be avoided due to potential welfare concerns.

Our evaluation of the effects of living in mixed species groups on the behavior and welfare of *Cebus* and *Saimiri* revealed no evidence of negative consequences for either species. Our results suggest that, with careful design and management of the environment, the formation of captive mixed species groups can have socially enriching effects, and be beneficial to welfare.

Based on observations of mixed species associations of *Cebus* and *Saimiri* in the wild [Terborgh, 1983], it was predicted that the smaller *Saimiri* would be more active in initiating associations, and would be more confident in using the outdoor enclosures when in mixed species groups. Our data did not support this prediction. No significant difference was found in the use of the outdoor enclosures by *Saimiri* when in single vs. mixed species groups. This may reflect each species being accustomed to being housed in a single species conditions before the mixed species group formation, being accustomed to being outdoors without the presence of the other, or from the limited risk of predation when in a captive environment. *Saimiri* were regularly present in the *Cebus* indoor enclosure suggesting some positive attraction to the *Cebus,* or their enclosure. The East *Cebus* group significantly increased their use of their indoor enclosure in the mixed condition, which appeared to result from their curiosity regarding the activity of the *Saimiri* present in their enclosure. Although West and East *Cebus* groups were considerably different in their use of the indoor and outdoor enclosures, the high numbers of scans in which both *Cebus* and *Saimiri* were simultaneously in the same enclosure was identical for West and East, suggesting that one common feature in both *Cebus* groups was a tolerant attitude toward *Saimiri*. This was so pronounced in the West group that a family group of three *Saimiri* became ''residents'' of the *Cebus* enclosure, in so far as they remained there to sleep at night (CCTV footage). Perhaps it was the frequency of their association with these individual *Saimiri* when in mixed species conditions that led the somewhat nervous West group of *Cebus* to venture outside only when the *Saimiri* were present.

These results suggest that although being in mixed species conditions did not produce substantial changes in their use of the enclosures, the presence of the other species appeared to hold some form of mutual attraction, and may have conferred a degree of increased confidence, although not in the way expected. Certainly, neither species made efforts to avoid the other, and the association was maintained despite the *Saimiri* having the option of segregating to their own enclosure if they were threatened. *Saimiri* were not the only active members of the association; *Cebus* actually initiated affiliative and neutral interspecific interactions more frequently than the *Saimiri*. Podolsky [1990] proposed that there were more advantages to the *C. apella* in their associations with *S. sciureus* than those suggested by Terborgh [1983]; such advantages may increase in captivity, where the competitive elements of the association are reduced.

As *C. apella* are approximately three times the size of *S. sciureus*, and are the dominant species in their associations in their natural habitat [Podolsky, 1990; Terborgh, 1983], the behavior and enclosure use of *Saimiri* was predicted to be adversely affected when *Cebus* were present. Of particular concern was whether interspecific aggression and displacements by *Cebus* would be present in the restricted captive environment, resulting in increased stress or even injury. However, the common forms of agonistic interactions observed were mild, and, contrary to expectations, were directed almost as frequently from *Saimiri* to *Cebus* as vice versa. Although the *Cebus* appeared to be the dominant species, the *Saimiri* were members of larger groups, making the dynamics of the dominance relationships often unclear. The only observation of an aggressive interaction involving physical contact occurred after a period of considerable time during which members of the West *Cebus* group had been attempting to displace unusually high numbers of (very active and vocal) *Saimiri*, who were in the preferred area of the *Cebus* enclosure. When attempts to displace them were proving ineffective, an adult female *Cebus* cuffed a young *Saimiri* who was resisting their efforts. This aggression was not typical and appeared to be resorted to only in order to reassert dominance in preferred territory. No significant changes were found in the substrate preferences of either species in single vs. mixed species groups, providing further evidence that the levels of displacement and aggression between the species did not raise concerns for the monkeys' welfare.

Well-being in single vs. mixed species groups was also assessed by examining changes in behaviors that are indicative of welfare. No significant changes were found in the percentage of *Cebus* engaging in allogrooming, nor either species' fast locomotion or play behaviors when in single vs. mixed species conditions. The presence of the other species thus did not have a negative impact on behavior. We were unable to collect data on scratching, a well established indicator of anxiety [Maestripieri et al., 1992], as it is a short duration event that was usually missed by scan sampling. The frequency of intraspecific aggression was less in mixed species groups, an effect that was particularly evident in the *Cebus* groups, for whom the rate per hour decreased threefold. However, we were unable to test this statistically.

Although a degree of aggression can be expected when housing primates in social groups, forms of social enrichment that are species appropriate and carefully implemented have been shown to improve the psychological well-being of primates in restricted captive environments and even reduce levels of aggression [Honess & Marin, 2006; Visalberghi & Anderson, 1993]. Such forms of social enrichment typically involve conspecifics, although the development of social enrichment options which consider the specific needs of different species are encouraged [Honess & Marin, 2006; Hosey, 2005]. The reduction of intraspecific aggression we observed suggests that the increased levels of social complexity and psychological stimulation when in mixed species associations had a positive effect. The rate of interspecific interactions per hour (>2.5) certainly suggests that the mixed species environment offers increased stimulation, with the interactions being evenly distributed between aggressive, affiliative, and neutral types. Based on the anecdotal report of a previously established mixed species group in captivity [Sodaro, 1999] the affiliative interactions were expected to occur more between youngsters, as was the case here for both affiliative and neutral interactions. It may be that as the interspecific relationships in the groups develop and as the youngsters mature to adults, aggression will decrease further and affiliation dominate.

Reviewing the effects of zoo environments on the behavior of captive primates, Hosey [2005] maintained that the zoo visitor experience and education is enhanced by watching animals behave in similar ways to the way they would in the wild. In their natural habitat, *Saimiri* have been found to occasionally benefit from the ability of *Cebus* to open hard *Scheelea* nuts; by foraging below the messy eaters, the *Saimiri* are able to gain the half-eaten nuts as they are dropped [Terborgh, 1983]. During observations in Phase 1, a young *Saimiri* repeatedly attempted to open a walnut, much to the amusement of watching visitors; as the effort proved fruitless, the walnut was dropped next to an adult female *Cebus*, who carried it to the rock area of the enclosure, cracked open the nut and allowed the young *Saimiri* to eat some pieces, inadvertently furthering the educational value of the exhibit. By Phase 2 of the observations, it had become a regular occurrence for groups of *Saimiri* to gather below individual *Cebus* who were eating whole apples, catching the fragments of apple that fell as they ate. Yet the affiliative behaviors between the *Saimiri* and *Cebus* that were observed, which included playing and passive food sharing, exceed those expected based on field observations [Podolsky, 1990]; the temporary nature of their associations and competition for resources most likely constrain the development of such a behavior in their natural environment. The affiliations that developed between the two species in Living Links demonstrate their ability to develop flexible social responses which vary according to the demands of their environment; the captive situation allows more time to engage in social interaction and sustain social relationships, while engaging in social interactions occupies time and energy in an environment that may be lacking in challenges and demands [Barrett et al., 2007]. The captive environment also allows one to detect and record subtle behaviors that may be missed in the wild [Hosey, 2005], which may be the case for our higher levels of interspecific interactions recorded in captivity compared with the wild [Podolsky, 1990].

Although aggressive interactions were relatively mild and infrequent, there were particular areas in the enclosures where aggressive events consistently took place. The data from Phase 1 indicated the locations that were preferred by both species, either as regular resting areas or for access to resources, which unsurprisingly, were typically the areas in which competitive situations arose, both between conspecifics and heterospecifics. Following the refurbishments, designed to increase the number of preferred sites and locomotory networks, and increase the areas in which resources were distributed in the enclosures, there was a significant decrease in the proportion of aggressive interspecific interactions observed. In the increasingly affiliative interactions, new forms of affiliative behavior were observed, including individual *Saimiri* and *Cebus* forming pairs who foraged and moved together for extended periods of time. Crows were observed stealing from scattered feeds in the East group's outdoor enclosures, only to be chased away by a subadult male *Saimiri* (alpha) and an adult male *Cebus* (also alpha), who by eye gaze and movement appeared to be coordinating efforts to drive the crow from the area (in the West group the same behavior was observed but performed by juvenile males of each species). In naturalistic enclosures such as these, the mixed species association may have similar benefits in relation to predators as in the wild, and as such, may be particularly important to the smaller and more vulnerable *Saimiri*. Although the vigilance of the *Saimiri* groups largely alleviated the initial concerns that young *Saimiri* may be at risk from mobbing crows and natural avian predators, the agitated reactions of *Saimiri* in response to avian movements that were observed when the *Cebus* were not outside suggested that their association with *Cebus* conferred increased confidence. It is also worth noting that although the affiliative interactions largely involved the youngsters in the West group in Phase 1, those recorded in Phase 2 were equally distributed between West and East groups, and involved adult individuals of both species. Having reduced levels of competition for resources and preferred areas, and with increased time to become accustomed to the other species, it became apparent that the mixed species affiliations are not restricted to the younger members of the groups.

When efforts are made to create captive environments that allow species to develop and display natural behavior, considering social environments that are typical to the species in their natural habitat can be most beneficial; utilizing our knowledge of their natural social group structures and carefully monitoring manipulations of social environments [McGowan et al., 2008; Visalberghi & Anderson, 1993] can have positive effects on the behavior and psychological well-being of captive primates. The creation of a suitable physical environment is equally critical; the size and complexity of the enclosures at Living Links appeared to play an imperative role in the successful formation of the mixed species groups. As proposed by Hardie et al. [2003], the key consideration in the formation of mixed species groups is whether the species would actively form associations in their natural environment. Few studies have been undertaken on the effects of housing primates with either primate or nonprimate species in mixed species groups [Hosey, 2005], making evaluations of their effect on welfare difficult, and leading the potentially enriching effects of the mixed species environments to be neglected. The groups of *C. apella* and *S. sciureus* in this study, and the groups of tamarin (*Saguinus*) species previously researched [Hardie & Buchanan-Smith, 1997; Hardie et al., 2003] show the high degree of cohesion that can develop in mixed species groups, demonstrating the mutual attraction of the association to the species involved. Interspecific interactions certainly seemed to enhance the experience of visitors to the exhibit, providing both an educational and enjoyable experience; researching this systematically would be of interest in the future. The effect of longer periods of association on the social relationships between *Cebus* and *Saimiri* in Living Links will be also be an area of future research and monitoring the effects of introducing new individuals to the groups will be of particular importance. The restrictions of the captive situation need not be detrimental to primates' welfare nor cause behavior too dissimilar to their wild counterparts [Hardie et al., 2003; Hosey, 2005]. Providing such a secure yet complex and stimulating social and physical environment may lead to novel behaviors and interspecific interactions emerging.

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