Journal of
Zoological and Botanical Gardens

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Space Use Preferences and Species Proximity in a Mixed-Species Zoo Monkey Exhibit

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Abstract

Many zoos display animals in mixed-species exhibits where multiple different species share the same space and potentially interact. This study analyzes a mixed-species exhibit with three New World monkey species (white-faced saki, black-capped squirrel monkey, and common squirrel monkey) at the Buffalo Zoo to determine the interactions among species and how different species use the exhibit space differently. Data were collected over twelve months using scan sampling. The sakis were more likely to be in proximity (less than 1.5 m apart) with others than were the squirrel monkey species. The sakis spent 26% of the time in contact with another animal, while both squirrel monkey species spent less than 1% of the time in contact with another animal. The squirrel monkeys used significantly more of the exhibit space than the sakis. A small number of observations occurred when only the sakis were on exhibit, and while speculative at best, anecdotally the sakis used much more of the exhibit when the squirrel monkeys were not on exhibit. There are many compelling reasons for zoos to design mixed-species exhibits; however, consideration needs to be given to how mixed-species exhibits impact animal behavior.

Keywords: exhibit design; mixed-species exhibits; primates; monkeys

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Academic Editor: Ashley N. Edes

Received: 3 July 2025
Revised: 20 August 2025
Accepted: 20 August 2025
Published: 22 August 2025

Citation: Chace, N.; Margulis, S.W. Space Use Preferences and Species Proximity in a Mixed-Species Zoo Monkey Exhibit. *J. Zool. Bot. Gard.* **2025**, *6*, 44. https://doi.org/10.3390/jzbg6030044

1. Introduction

Many zoos exhibit multiple species, including primates, within the same exhibit, however there is little research available on how living in a mixed-species zoo environment impacts the animals' behavior, space use, and social interactions. One past study on a mixed-species exhibit with Goeldi's monkeys (*Callimico goeldii*) and pygmy marmosets (*Callithrix (Cebuella) pygmaea*) found that the two species differed in how they used the exhibit space provided and that interactions between individuals were rare and never affiliative [1]. Similarly, a study on brown capuchins (*Sapajus apella*) and common squirrel monkeys (*Saimiri sciureus*) found that both species interacted with conspecifics much more frequently than with heterospecifics [2]. Other studies on mixed-species primate exhibits have primarily focused on the behavior surrounding a new species being introduced to a mix [3,4]. Another study focused on how one primate species, Senegal bushbabies (*Galago senegalensis*), and two non-primate species interacted with the same environmental enrichment items differently in a mixed-species exhibit [5].

While mixed-species exhibits can be beneficial to welfare as highly complex and enriching environments, there are also potential negative welfare implications to mixed-species exhibits [6]. While some potentially negative welfare implications may be obvious, such as a mortality event or significant injury, without thorough scientific research, other negative impacts, such as heightened stress levels or agonism, may go unnoticed. Some studies on primates in mixed-species exhibits have focused on studying one species across multiple mixed-species exhibits. These studies generally found great variability in the success of mixed-species exhibits with ring-tailed lemurs (*Lemur catta*) or talapoin monkeys (*Miopithecus ogouensis*) based on various factors such as exhibit size, group composition, and what other species are mixed [7,8]. As such, it is important that more zoos consider evaluating and researching how animals use the space provided in mixed-species exhibits as there is not a uniform trend across all exhibits or all species. Evaluating and studying individual exhibits offers the best opportunity to fully understand how the mixed-species environment impacts those individual animals, and whether there are negative welfare implications for the species chosen. Even if a particular mixed-species exhibit is successful at one zoo, this does not mean that it would be successful if attempted at a different zoo or with different individuals due to the numerous factors that determine success. It is important to fully understand these effects so that zoo managers can consider the behavioral impact of mixed-species exhibits when evaluating their zoo's animal well-being programs, collection plans and designing future exhibits.

Space use is commonly studied as a metric of enclosure use and as a means to assess zoo exhibits [9]. Multiple different metrics are used to study space use, with one common metric being zone occupancy, where an enclosure is categorized into zones and animal zone is recorded through either focal animal or scan sampling techniques. Another metric to study space use is the modified spread of participation index, which is used to quantify the evenness of enclosure use [10]. While the modified spread of participation index has been used in a past study on mixed-species exhibit space use, this metric requires detailed measurements of enclosure zones that may be difficult to access [11]. Here, we opted to quantify space use with an electivity index, which, while less frequently used in zoo studies, can be used to determine which exhibit zones are under- or over-utilized [9,12]. Electivity indices have been used in several zoo studies, including measuring the impact of moving to a new, more naturalistic exhibit on space use in chimpanzees (*Pan troglodytes*) and Western lowland gorillas (*Gorilla gorilla gorilla*) [13] and determining whether siamangs (*Symphalangus syndactylus*) have a preference for horizontal supports over vertical supports [14].

Space use studies are important as they can help identify what exhibit features animals show a strong preference for or avoidance of, such as one paper which found gorillas tend to avoid open spaces in their exhibit [13]. Another paper on space use found sitatunga (*Tragelaphus spekii*) showed a preference for exhibit zones that the authors deemed "biologically relevant", especially a riverbank section of the exhibit [15]. Understanding which sections of zoo exhibits animals show a strong preference for can be important in informing future exhibit design, especially if exhibit quality is prioritized over exhibit quantity [16]. Space use studies are also often highly relevant as a form of post-occupancy evaluation to assess newly constructed exhibits [17]. Studying zoo animal space use is also important from the perspective of zoo visitors as it is desirable for animals to prefer spending time in parts of exhibits that are easily visible to visitors.

This study focuses on the space use and interactions between individuals in a mixed-species exhibit of three New World monkey species at the Buffalo Zoo. Two of these species are very close relatives, the common squirrel monkey (*Saimiri sciureus*) and black-capped squirrel monkey (*Saimiri boliviensis*), while the third species, white-faced sakis (*Pithecia pithecia*), is in a different family. This mixed-species exhibit was already established prior to the beginning of the study. The European Association of Zoos and Aquariums' (EAZA) Best Practice Guidelines for sakis indicate that they are a tolerant species that are ideal for mixed-species exhibits and have been successfully mixed with a variety of primate and non-primate species [18]. Neither the European Association of Zoos and Aquariums nor the Association of Zoos and Aquariums (AZA) have published mixed-species guidelines for squirrel monkeys, although a variety of zoos house them in mixed-species settings [19].

Neotropical primates, especially squirrel monkeys, have also been observed to frequently form mixed-species assemblages in the wild, benefitting from shared vigilance and foraging opportunities, making them a promising option for zoos to create naturalistic mixed-species exhibits [20]. However, squirrel monkeys form mixed-species assemblages most frequently with capuchin monkeys rather than sakis. Mixed-species assemblages between squirrel monkeys and capuchins have been observed repeatedly across multiple different species of *Saimiri* [20,21]. That said, not all squirrel monkeys form mixed-species assemblages in all portions of their range, with field research in Central America noting that *Saimiri oerstedii* was not observed to form mixed-species assemblages with brown capuchins, indicating mixed-species assemblages may only be beneficial under certain ecological conditions related to anti-predation and/or foraging opportunities [22]. One study found that buffy sakis (*Pithecia albicans*) frequently formed mixed-species assemblages with multiple tamarin species (*Saguinus* sp.) [20]. While reports of *Pithecia* in mixed-species assemblages are not as common as *Saimiri*, this could be due to the fact *Pithecia* are difficult to study in the wild [23]. Given that shared foraging opportunities are often a component of mixed-species assemblages, the fact *Pithecia* specialize in seed-eating may also contribute to their lack of mixed-species assemblages [24].

White-faced sakis and common squirrel monkeys have ranges which closely overlap in Guyana, Suriname, French Guiana, and Brazil [25,26]. Black-capped squirrel monkeys do not have an overlapping range with either species, however they do overlap with other members of genus *Pithecia*, such as the Ryland's bald-faced saki (*Pithecia rylandsi*) in northern Bolivia [27,28]. While past studies have noted that mixed-species exhibits with sympatric monkey species tend to have a higher success rate, zoos are often limited by species availability and the limited number of species recommended for management by the AZA [19]. As a result, oftentimes zoos opt to design exhibits that encompass broad geographic areas (e.g., South America) rather than narrowly tailoring exhibits to solely feature sympatric species.

White-faced sakis are often believed to be pair-living, although some research has reported as many as three females living together without reproductive suppression [29,30]. On the contrary, squirrel monkeys are more gregarious and live in large, multi-male, multi-female groups [31]. While common and black-capped squirrel monkeys are closely related, there are some differences in their ecology, with black-capped squirrel monkeys having larger home ranges and living in larger groups than common squirrel monkeys [32,33]. Common squirrel monkey groups typically number from 15–50 individuals, while black-capped squirrel monkey groups number 45–75 individuals. Female-female aggression has been observed more often in black-capped squirrel monkeys than common squirrel monkeys [32,33].

We predict that intraspecific interactions will be more common than interspecific interactions in the mixed-species exhibit investigated here. Similarly, we also predict that different species will differ in their space use and in their proximity to heterospecifics versus conspecifics. Further, we predict that the two squirrel monkey species will be more similar in space use than the less closely related sakis.

2. Materials and Methods

2.1. Study Site and Subjects

This study took place at the Buffalo Zoo, where black-capped squirrel monkeys, common squirrel monkeys, and white-faced sakis live in a shared indoor exhibit in the M&T Bank Rainforest Falls building. The exhibit measures 56 square meters, with an accessible height of 7.6 m [34]. The exhibit is home to three white-faced sakis, who were identified as individuals, two black-capped and two common squirrel monkeys, each identified only by species, and a red-footed tortoise (*Chelonoidis carbonaria*) who was not included in the study. The two species of squirrel monkey are managed as a single group and housed together at all times, both on and off exhibit. All animals were housed together on exhibit from approximately 9:30 and 14:30. Prior to release on exhibit, squirrel monkeys and sakis were fed their primary diet in separate holdings, while an additional foraging diet of 140 g was available on-exhibit. Details about the individual animals can be found in Table 1.

Table 1. Animals in the Mixed-Species Primate Exhibit.

Species	Sex	Date of Birth [35,36]	Notes	When Introduced
White-faced saki	Male	10 April 2003	Father of younger male saki	These two species were introduced to one another in August 2017
White-faced saki	Female	8 March 2006	Mother of younger male saki	
White-faced saki	Male	28 April 2010	Adult offspring of saki pair	
Black-capped squirrel (n = 2)	Female	8 April 2012 5 June 2012	Animals not identified individually	
Common squirrel (n = 2)	Female	18 June 2004 9 September 2005	Animals not identified individually	This species was added to the established mix in February 2023
Red-footed tortoise	Male	Unknown	Omitted from study	

2.2. Data Collection

Data for this study were collected between January 2024 and January 2025, following a four-month trial period to perfect the methodology and ensure researcher reliability. We used instantaneous scan sampling to observe all individuals at two-minute intervals for a total of ten minutes [37]. All animals were observed simultaneously on each scan and during each observation. Observations were recorded using the app ZooMonitor version.4.1 [38]. During each scan, we recorded the behavior, location, and both distance and species of the two closest neighbors for all seven monkeys. 96 observations were completed when all animals were present, in addition to thirteen observations where only the sakis (n = 6) or only the two squirrel monkey species (n = 7) had exhibit access. Observations with all species present were made over 94 days between January 2024 and January 2025, ranging between three and ten observations per month of the study. Data with all animals present totaled sixteen hours. All scans occurred between 9:30 and 14:30. Nineteen observations with all animals, one of the saki only observations, and five of the seven squirrel monkey only observations occurred on days that the Buffalo Zoo was closed to the public during the off-season. Inter-observer reliability was assessed by simultaneous data collection with all collectors prior to contributing data.

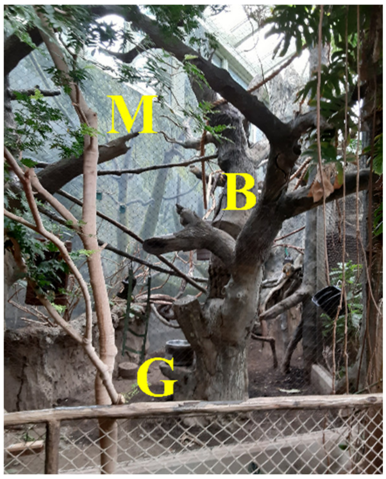
2.3. Location Data

Location was recorded as either out of view or any of five sections of the exhibit detailed in Table 2, and a map highlighting these locations can be found in Figure 1.

Table 2. Locations in the mixed-species monkey exhibit.

Location	Description
Saki Corner	Animal is in the top corner in the far right of the habitat, near the shift doors. Named "Saki Corner" because the sakis usually stayed in this section of the exhibit.
Window Ledges	Animal is on the window sills in the back of the exhibit.
Mesh	All four limbs of the animal are on the mesh fencing at the front or top of the exhibit.
Ground	Animal is on the ground.
Branches	Animal is on the branches in the middle of the habitat, or is in one of the hanging hides attached to the branches.
Out of View	Animal cannot be seen and location is not known.

Upper View



Lower View

Figure 1. Images of the mixed-species exhibit from the upper (**left**) and lower (**right**) viewing areas with the five locations labeled: Branches-B, Ground-G, Mesh-M, Saki Corner-S, Window Ledges-W.

2.4. Neighbor Data

On each scan, the distance and species of the two closest neighbors of each animal were recorded. A neighbor was defined as any animal within 1.5 m of the focal animal. The distance from the two closest neighbors was defined as either contact, close neighbor, distant neighbor, or no neighbor, described in Table 3. The distance was a visual estimate, not an exact measurement.

Table 3. Distance From Closest Neighbor Category Descriptions.

Location	Description
Contact	Individual is in direct contact with another individual (e.g., touching)
Close Neighbor	Individual is within 0.5 m.
Distant Neighbor	Individual is between 0.5–1.5 m.
No Neighbor	Closest individual is further than 1.5 m.

2.5. Behavioral Data

On each scan, the behavior of each animal was recorded. The selected behaviors on our ethogram are defined in Table 4. Behavior was not a main focus of our study, however we examined the percentage of time observed engaged in social behaviors (affiliation and agonism), as this may relate to potential neighbor patterns.

Table 4. Selected Behavioral Ethogram.

Behavior	Description
Locomotion	Animal is moving around the exhibit.
Inactive	Sitting, standing, or laying while not active in physical activity.
Enrichment Use	Manipulating or interacting with any object in the exhibit provided by keepers.
Affiliation	Allogrooming or other positive behavior towards another individual.
Agonism	Any aggressive behavior targeted at another individual, such as chasing, contact, and non-contact aggression.
Forage	Eating or procuring food.
Self-Directed Behaviors	Auto-grooming, scratching, urinating, defecating, or any other manipulations.
Out of View	Focal animal is not in the observer's field of view.

2.6. Data Analysis

Kruskal–Wallis tests were performed in jamovi version 2.3.21 [39]. Figures were created in Microsoft Excel. Given that we did not identify the squirrel monkeys as individuals, all statistical tests were performed at the species level without regard to the individual animal.

In analyzing space use, we omitted out of view observations and omitted the locations "ground" and "window ledges" as these were rarely used. For the three remaining locations (mesh, branches, saki corner), we performed a Kruskal–Wallis test to determine if there was a statistically significant difference in the percentage of time each species was observed in that location, as well as Dwass-Steel-Critchlow-Flinger (DSCF) pairwise comparisons to determine which species differed significantly. Additionally, we also calculated a Vanderploeg and Scavia Electivity Index to quantify space use [9,12,13]. Because we were not able to accurately measure the irregularly shaped exhibit, we estimated the approximate proportion of usable space in each zone. There were a small number of observations where only sakis or only the two squirrel monkey species were on exhibit, and these were analyzed separately. No statistical tests were performed due to the small number of such observations ($n = 6$ and $n = 7$, respectively).

In analyzing neighbors, we performed a Kruskal–Wallis test and DSCF pairwise comparisons to analyze whether there was a difference in the distance to the closest neighbor across species, without regard to what species the closest neighbor was. Distance from closest neighbor was treated as an ordinal variable based on our categories described in Table 3.

To determine if the species neighbor was significant, we calculated a chi-square test of independence, with the expected values calculated based on the number of individuals that were possible neighbors. For example, a black-capped squirrel monkey had the possibility of being a neighbor to three sakis, two common squirrel monkeys, or one black-capped squirrel monkey so the expected values followed a ratio of 3 saki: 2 common: 1 black-capped rather than equivalent values. To calculate expected values, we multiplied the total number of neighbors a species had by the fraction of possible neighbors of the neighbor species. For example, since two of the six possible neighbors a saki could have been sakis, the expected value was calculated as (total number of times a saki had a neighbor) × (2/6). Significance of the chi-square tests of independence were determined using an online calculator from Social Science Statistics [40]. Observations with no neighbors were omitted from this test, and the observed values were the frequency that each species was a neighbor, regardless of whether they were a close or distant neighbor.

We did not analyze differences in behavior as this was not an overall focus of our study. We report species-specific percentages of social behavior for comparative purposes.

3. Results

3.1. Space Use When Together

When all three monkey species share the exhibit, there were some notable significant differences in space use. The percentage of time observed in each location can be seen in Figure 2. The white-faced sakis spent almost all of their time in the saki corner and were never seen on the mesh. Both the black-capped and common squirrel monkeys spent the majority of their time on the branches and overall utilized a larger amount of the exhibit space than the white-faced sakis.

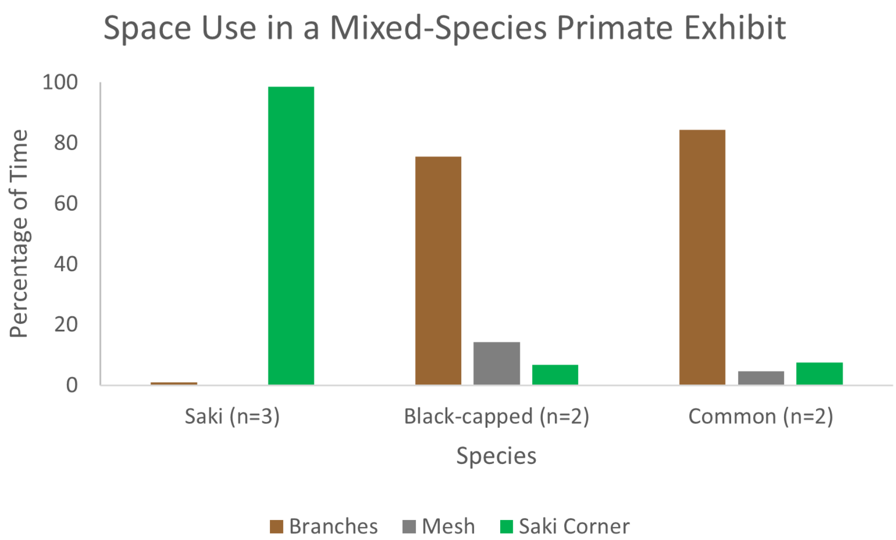


Figure 2. Percentage of time each species was observed at the three locations analyzed. All results are statistically significant except for comparing black-capped and common squirrel monkeys in the Saki Corner. Statistically significant results are marked with asterisks.

We performed three Kruskal–Wallis tests to determine if there was a statistically significant difference in the percentage of time each species was observed in the branches, mesh, and saki corner and all three tests were significant (Branches: $\chi^2 = 526.28$, df = 2, $p < 0.001$; Mesh: $\chi^2 = 153.79$, df = 2, $p < 0.001$; Saki Corner: $\chi^2 = 402.77$, df = 2, $p < 0.001$).

Our DSCF pairwise comparisons indicated that all results were statistically significant to a *p*-value of less than 0.017 except for the difference in the percentage of time the black-capped and common squirrel monkeys were observed in the saki corner (see Figure 2). Sakis spent significantly more time in the saki corner than either squirrel monkey species, and both squirrel monkey species spent significantly more time on the branches and mesh than the sakis. When comparing the two squirrel monkey species, the black-capped squirrel monkeys spent significantly more time on the mesh and common squirrel monkeys spent significantly more time in the branches. There was no significant difference in the amount of time each squirrel monkey species spent in the saki corner.

In addition to the Kruskal–Wallis tests, we also calculated an electivity index for each species in all five exhibit zones. The results of the electivity indices are shown in Table 5. Results above 0.4 typically indicate a strong preference for that location, and results under −0.4 typically indicate a strong avoidance of that location. All results above 0.4 or under −0.4 are bolded in the table. White-faced sakis showed a strong preference for the saki corner and strong avoidance of all other locations. Both squirrel monkey species showed strong preferences against the ground and saki corner, while the common squirrel monkeys also showed a strong preference against the mesh.

Table 5. Results of an Electivity Index for all three species in all zones of the exhibit. Results that show a strong preference for (>0.4) or against (<−0.4) a location are bolded.

Location	White-Faced Saki (n = 3)	Common Squirrel (n = 2)	Black-Capped Squirrel (n = 2)
Saki Corner	**0.66**	**−0.46**	**−0.49**
Branches	**−0.96**	0.26	0.20
Window Ledges	**−0.89**	−0.26	−0.34
Mesh	**−1.00**	**−0.53**	−0.03
Ground	**−1.00**	**−0.88**	**−0.88**

3.2. Space Use When Separated

A small number of observations occurred when only the sakis (n = 6) or two squirrel monkey species (n = 7) had exhibit access. While there were not enough data to perform any statistical tests, the results did show that the white-faced sakis differed in their space use when all three species were together versus when only the sakis were on exhibit, spending the majority of time in the saki corner when together but the majority of time on the branches when separate. The differences in space use for the two squirrel monkey species were less substantial. Figure 3 shows the space use of the two squirrel monkey species when the sakis were not on exhibit, while Figure 4 shows the behavior of the sakis when the squirrel monkeys were not on exhibit.

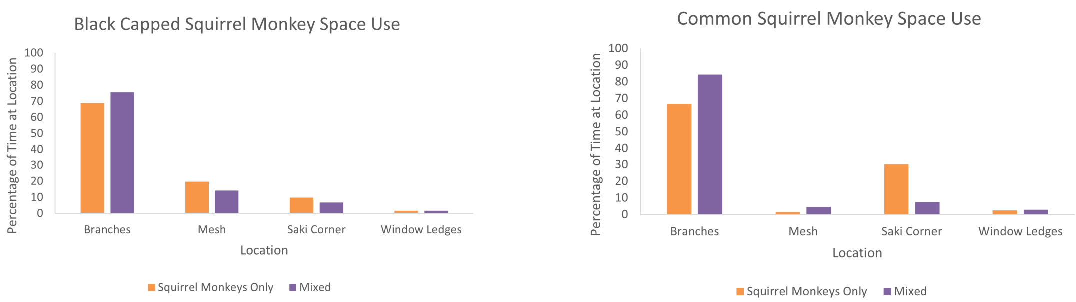


Figure 3. Percentage of time the black-capped (**left**) and common (**right**) squirrel monkeys were observed at each location when only squirrel monkeys were on exhibit or when the exhibit was mixed with sakis.

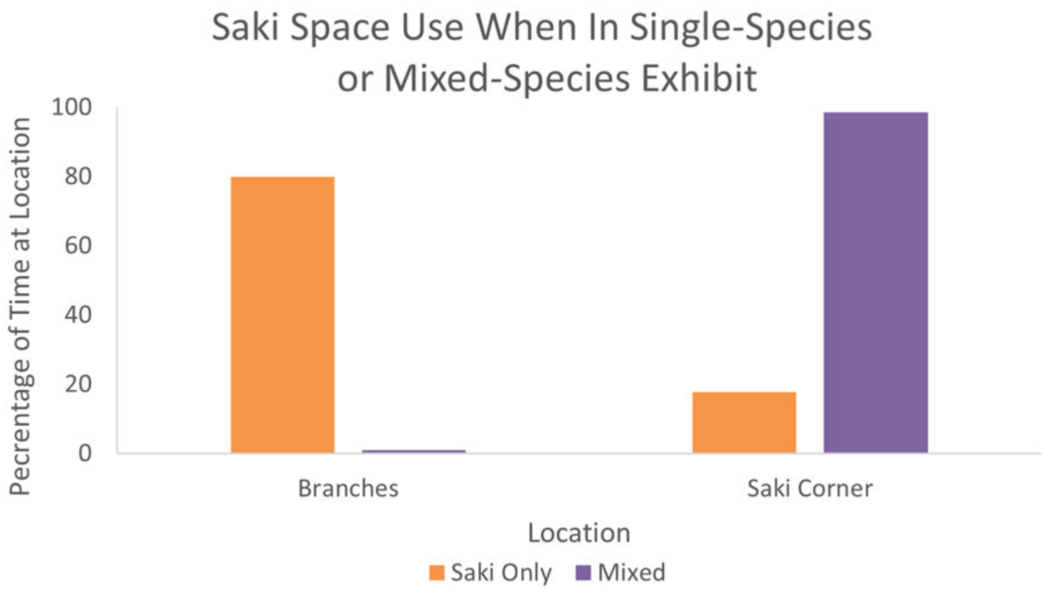


Figure 4. Percentage of time the white-faced sakis were observed at each location when the enclosure was single-species versus mixed-species. Locations not used by the sakis have been omitted from the figure.

When only the squirrel monkeys were on exhibit without the sakis, the common squirrel monkeys spent less time on the branches (0.667 instead of 0.843) and more time in the saki corner (30.1% versus 7.5%). The black-capped squirrel monkeys also spent slightly more time in the saki corner when separate (9.8% versus 6.8%) and less time on the branches (68.9% versus 75.5%). The black-capped squirrel monkeys spent more time on the mesh when separate (19.7% versus 14.2%), while the common squirrel monkeys spent less time on the mesh (0.16% versus 4.7%). Given the small number of observations, it is unclear whether these results reflect that the squirrel monkeys choose to spend more time in the saki corner instead of the branches when the sakis are not on exhibit or whether the difference is due to random chance.

The difference in space use when the white-faced sakis were in a single-species or mixed-species exhibit was more pronounced than in the squirrel monkeys. When in a single-species exhibit, the sakis spent the majority of their time on the branches (0.800), while in a mixed-species exhibit the sakis spent the majority of their time in the saki corner (0.986).

3.3. Neighbor Distance

Distance to closest neighbor was treated as an ordinal variable based on our categories shown in Table 3. Our results of the Kruskal–Wallis test were significant ($\chi^2 = 928$, df = 3, $p < 0.001$), and the DSCF pairwise comparisons indicated that there were significant differences between the saki and common squirrel monkeys (W = 34.98, $p < 0.001$) and between the saki and black-capped squirrel monkeys (W = 35.63, $p < 0.001$). There was no significant difference between the black-capped and common squirrel monkeys (W = -1.81, $p = 0.406$). Not only did the sakis have a neighbor more frequently than either squirrel monkey, but on instances where they had a neighbor, that neighbor was significantly more likely to be a closer neighbor or in contact than a squirrel monkey's neighbor was (Figure 5).

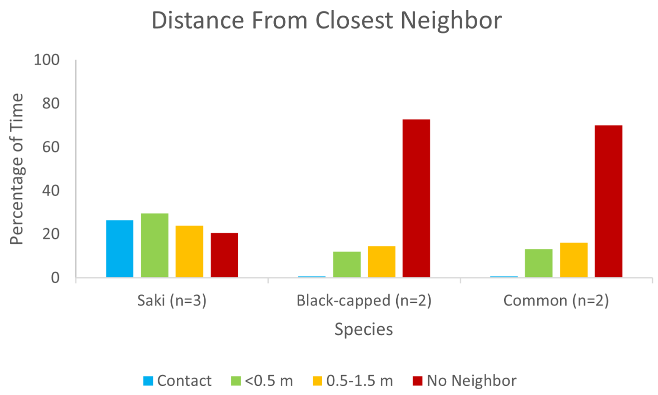


Figure 5. Percentage of scans where each animal's closest neighbor was in each distance category, regardless of the species of that neighbor. The closest neighbor of a white-faced saki was significantly more likely to be closer than was a neighbor of either a black-capped or common squirrel monkey, but there is no significant difference between the two squirrel monkey species.

3.4. Neighbor Species

A chi-square test of independence was calculated, where the expected values were calculated based on the proportion of possible neighbors for each species, as described more fully in Section 2.6. A total of 2218 instances where an animal had a neighbor were observed. There was a statistically significant difference in what species was a neighbor ($\chi^2 = 3368.756$, df = 4, $p < 0.001$). All three species were more likely to be with a conspecific than would be expected by chance. However, both squirrel monkey species were also more likely to be with the other squirrel monkey species than expected, but by smaller amounts than with their own species. Figure 6 shows the frequency with which each species was a neighbor adjusted for the number of individuals of each species. The most common combination of neighbors was two sakis as neighbors, occurring on 1577 total scans (788.5 scans on average per individual). 63% of total instances with a neighbor were between two sakis. The second most common combination of neighbors were two common squirrel monkeys, occurring on 142 scans.

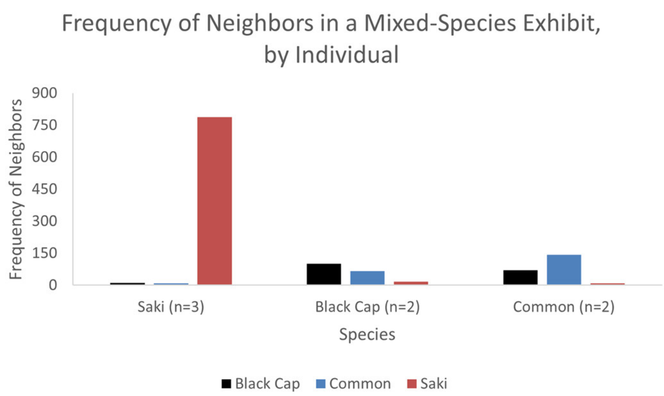


Figure 6. Frequency that each species was a neighbor per individual. This was calculated by dividing the number of scans in which the species was a neighbor by the number of individuals of that species that were possible neighbors. Results of all the chi-square tests were statistically significant.

3.5. Behavior

Agonism was too rare to be analyzed, as it was only observed six times in total across all species and across all 96 observations. With the exception of a singular black-capped squirrel monkey scan, affiliation only occurred in white-faced sakis, and it comprised 23.7% of their activity budget. Anecdotally, most of the affiliative behavior we observed in white-faced sakis was allogrooming.

4. Discussion

Our results indicate that living in a mixed-species zoo environment can impact the space use and social environment of New World primates. Our study supports previous research on mixed-species exhibits that indicate individual monkeys interact with conspecifics at a higher rate than they interact with heterospecifics [1,2]. The sakis were significantly more likely to have a closer neighbor than the squirrel monkeys, however it is unclear how much of this difference is due to species-specific behavior or due to the mixed-species environment. Since white-faced sakis are a pair-living monkey species, it would be species-typical for them to engage in affiliative behaviors at a higher rate than would the more gregarious squirrel monkeys [29,31]. However, given that the sakis showed a strong preference for the saki corner, which is a much smaller space than the branches area, some of the difference in neighbors could be that avoiding the squirrel monkeys necessitates being in closer proximity to one another. Given that the sakis spent more time in other spaces when they were the only species on exhibit, this suggests that their preference for the saki corner is not due to habitat-related factors such as height. In this study, the sakis spent 23.7% of scans participating in affiliative behavior (most typically allogrooming). At least some of this difference may be due to species-specific behavior patterns and not due to the mixed-species environment. However, in past research on wild white-faced sakis, the animals spent far less time engaging in allogrooming and were in proximity to other individuals less often than in our study [41]. Given the unexpectedly high affiliation rates in sakis, more research into social behavior in zoo-housed sakis may be an interesting area for further investigation.

There were some differences in space use between the black-capped and common squirrel monkeys, most notably that the common squirrel monkeys showed a strong avoidance of the mesh, however it is unclear how much of this difference is due to the mixed-species environment, species-specific behavior, or individual life histories. The two black-capped squirrel monkeys came to Buffalo Zoo from a lab setting, while the two common squirrel monkeys came to Buffalo Zoo from another AZA-accredited zoo. It is possible that the black-capped squirrel monkeys at the Buffalo Zoo spent more time on the mesh than did the common squirrel monkeys because they are interested in people due to their lab upbringing [42]. Another possibility is that the difference in space use between the black-capped and common squirrel monkeys is that the two common squirrel monkeys are both geriatric individuals, while the black-capped squirrel monkeys are both younger. Although we were not able to reliably identify the squirrel monkeys as individuals, conspecific behaviors were consistent with little variation. More detailed observations on known individuals, such that age, gender, rearing condition, and housing history could be included as covariates, would be a valuable contribution to a larger study.

Differences in space use when only one group was on exhibit were most noticeable in the white-faced sakis, who spent the vast majority of time in one corner of the exhibit (dubbed the "saki corner") when mixed with the squirrel monkeys, but on the rare occasions where they were not mixed spent more time on the branches in the lower portion of the exhibit. The six observations with only sakis on display occurred at a variety of times of day, which rules out a temporal difference in location preference as an explanation for the difference. Additional data with only the sakis on exhibit would serve to solidify this finding. Furthermore, when one of the squirrel monkeys did enter the saki corner, we anecdotally observed that the sakis would sometimes move to the other side of the saki corner and avoid the squirrel monkey, potentially indicating that the sakis prefer the saki corner as a form of avoidance behavior. The sakis were never observed on the mesh during our study, however they have been observed to use the mesh, according to zoo staff, so they are capable of doing so [43]. While there were not enough data to run any statistical tests, the substantial difference in location when only sakis were on exhibit and additional anecdotal evidence leads us to speculate that the trend would continue with further data.

Ideally, more observations with only the saki or squirrel monkeys on exhibit would have allowed us to more clearly determine if the observed differences were statistically significant, however this scenario occurred rarely. One study compared the behavior of Parma wallabies (*Macropus parma*) housed in a mixed-species exhibit and in a single-species exhibit and found that the wallabies in the single-species exhibit spent significantly more time foraging and used more of their enclosure than the wallabies in a mixed-species exhibit [44]. This result further supports that zoo animal behavior is impacted by living in a mixed-species environment, including in ways that would only be noticeable when comparing their behavior in different environments. The wallabies used more of their enclosure in the single-species exhibit, similar to our finding that the white-faced sakis used more of their enclosure when they were the only primates on-exhibit.

A study comparing common squirrel monkeys and brown capuchins housed in a mixed-species exhibit versus a single-species exhibit found that the squirrel monkeys did not significantly differ in their space use when housed with the capuchins versus in a single-species exhibit [45]. This supports our observations with only squirrel monkeys on exhibit, where the differences in space use were less pronounced than the difference in saki space use. While more observations would be needed to draw any definitive conclusions, it is likely the differences seen were due to the small number of observations and not due to actual differences in the squirrel monkeys' space use. It is unclear whether there would be any observed differences with only one of the two squirrel monkey species out, but we were not able to observe this given the zoo manages the squirrel monkeys as a single group. Given that squirrel monkeys are known to often form mixed-species assemblages in the wild, it is possible that their species-typical behavior is less dependent on the presence of other monkey species than would be expected for saki monkeys, who tend to live in small family groups [19,20].

Given the popularity of mixed-species exhibits in zoos, and the differing results across past research on the subject, future research on how mixed-species environments impact zoo animal behavior is warranted. Even amongst the two closely related squirrel monkey species, individuals were more frequently neighbors with their conspecific than with a heterospecific. However, more research is needed to determine whether this is because squirrel monkeys prefer conspecific companions over heterospecific squirrel monkey companions or whether the difference is the result of other factors such as age or social upbringing. While research comparing common and black-capped squirrel monkeys is rare, one paper did indicate multiple differences in the personality of a black-capped and common squirrel monkey that could explain why they would prefer being near a conspecific [46]. Other studies have found female-female aggression to be more common in black-capped squirrel monkeys than common squirrel monkeys, and while agonistic behaviors were very rare in our study it is possible this is related to the squirrel monkeys preferring conspecific companions [32,33]. Especially given that common and black-capped squirrel monkeys are known to hybridize in captivity, it would be useful for future studies to examine whether squirrel monkeys display a preference for a conspecific squirrel monkey over a heterospecific squirrel monkey [47].

Our research also supports the results of a previous study which found that brown capuchins and common squirrel monkeys differed in their space use in a mixed-species exhibit [11]. However, that paper found the squirrel monkeys stayed in peripheral sections of the enclosure, which is the opposite of how the squirrel monkeys behaved in our study. The authors provided two possible explanations for the squirrel monkeys remaining in peripheral areas: a preference due to habitat functionality and/or the squirrel monkeys engaging in avoidance behaviors. If the squirrel monkeys were choosing to use peripheral areas due to habitat functionality, then the fact our exhibit was smaller, strictly indoors, and differed in design could mean their preferred foraging locations and/or other desired resources were located closer to the center of our exhibit. If the squirrel monkeys were choosing to use peripheral areas out of avoidance, the fact we did not observe avoidance behavior could be because white-faced sakis are smaller than capuchins and live in smaller groups.

While this paper, like much of the scientific literature on mixed-species exhibits, focuses on primates, the methodology is not primate-specific and could be used for studying mixed-species exhibits with other taxa. Given the range of positive and negative outcomes for mixed-species exhibits, it would be especially useful to apply this methodology to common mixed-species exhibits that are under-studied, such as those for birds or fish [19]. Few studies exist on birds in mixed-species exhibits, however one of the papers indicated mixed success and heightened aggression in introducing great blue turacos (*Corythaeola cristata*) to a large aviary, further showing that there is a need to evaluate more of the existing mixed-species aviaries and research the impact of the mixed-species environment on bird behavior and welfare [48]. Another study on birds in a mixed-species exhibit found that three species of African birds were responsive to an enrichment program intended for the Western lowland gorillas (*Gorilla gorilla gorilla*) that shared their exhibit [49]. It would also be useful to study the existing mixed-species exhibits with species that are seldom found in such exhibits, for instance large carnivores, as studying these exhibits would help determine their effectiveness and whether or not replicating similar exhibits in the future is a good idea [50].

We believe that the methodology described in this paper could be broadly applicable to studying space use and the interactions between individuals in zoo mixed-species exhibits, regardless of the specific taxa displayed. This methodology does not require the ability to identify individuals, making it particularly useful for exhibits or for species in which individual identification may not be possible, and is not time-intensive, making it useful for zoo professionals who may only have ten minutes to spare. Incorporating behavioral monitoring into keeper routines is beneficial to both animals and animal care staff. It can provide an indication of individual animal welfare as well as offer keepers an opportunity to carefully observe their animals. Overall, the results of our study highlight that living in a mixed-species zoo exhibit can have subtle implications on animal space use and interactions between individuals, and that these differences may often go unnoticed without detailed behavioral monitoring.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jzbg6030044/s1, Table S1: Zoo Monitor data.

Author Contributions: Conceptualization, S.W.M. and N.C.; methodology, S.W.M. and N.C.; software, S.W.M.; validation, S.W.M.; formal analysis, N.C. and S.W.M.; investigation, S.W.M. and N.C.; resources, S.W.M.; data curation, S.W.M.; writing—original draft preparation, N.C.; writing—review and editing, S.W.M.; visualization, N.C.; supervision, S.W.M.; project administration, S.W.M.; funding acquisition, S.W.M. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Ethical review and approval were waived for this study following consultation with the Canisius University IACUC Chair, as it was deemed that the specific non-invasive observational protocol used in this study did not require approval or oversight by the IACUC.

Data Availability Statement: The datasets analyzed during the current study are available as Supplementary Materials.

Acknowledgments: The authors thank the keepers, curators, and administration of the Buffalo Zoo for providing access to the zoo's collection for this study. We are grateful for their assistance in all ways. We thank Abigail Gurgol for assistance in data collection. N.C. was supported by a Canisius Earning Excellence Program fellowship. We thank four anonymous reviewers for helpful comments on an earlier version of this manuscript.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

AZA	Association of Zoos and Aquariums
DSCF	Dwass-Steel-Critchlow-Flinger Pairwise Comparisons
EAZA	European Association of Zoos and Aquariums

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