

**A comparative study on the
behavioural effects of a mixed-species
enclosure on capybaras (*Hydrochoerus
hydrochaeris*) at Blackpool Zoo, UK**



Abstract

The prevalence of mixed-species enclosures (MSEs) in modern day zoos provides ample opportunity to study how captive animals behave interspecifically. However, not all species are suited to interspecific co-habitation (e.g., due to similar niche occupancy, competition for resources) and incompatible mixing often leads to increased stress behaviour and frequency of agonistic interactions. It is therefore crucial that research surrounding captive animal behaviour (including interspecific interactions) within enclosures is applied to ensure the optimal conditions for that species is provided. The aim of this study was to assess the behaviour of three groups (A, B and C) of capybara (*Hydrochoerus hydrochaeris*) housed within separate MSEs at Blackpool Zoo, UK. Specifically, to highlight any behavioural differences and attempt to evaluate the success of the partner species to co-habit alongside capybaras. Scan-sampling observations were taken within each enclosure, observing behaviour, location selection and proximity to the nearest member of the partner species. Location selection was similar across groups, with grassland and indoor & feeding troughs dominating. Behaviour was also similar across enclosures, as inactive and feeding behaviours were exhibited the most. Agonistic behaviours were observed within closest proximity to Patagonian mara (*Dolichotis patagonum*), spider monkey (*Ateles fusciceps robustus*) and lowland tapir (*Tapirus terrestris*). The mara was on average closest to the capybaras ($7.9\text{m} \pm 7.42$) and the spider monkey the furthest ($23.5\text{m} \pm 9.03$). Capybara behaviour (and location) was associated with the partner species present, yet the proximity between the two species had no effect on it. The partner species present also did not determine proximity between themselves and the capybaras. In summary, partner species within a MSE does affect captive capybara behaviour to some extent, the factors modulating the effects are less clear. A lack of behavioural deviances denoting the directionality of interspecific relationships does not warrant considering a change in enclosure environments at Blackpool Zoo to improve welfare. Although further research is recommended to corroborate this.

1. Introduction

1.1. Mixed-species enclosures (a zoological concept)

Today, mixed-species enclosures (MSEs) are more prevalent in zoological collections worldwide than is or has ever been reported in animal welfare literature (Green *et al.*, 2022). Modern-day justification for MSEs stems from a combination of efficiency in management practices, maximising space utilisation and funding, enhancing visitor experience and improving animal enrichment practices (Probst and Matschei, 2008). In spite of any benefits, costs with respect to the welfare of those animals involved must be considered before proceeding with establishing a MSE. Some species may not be suited for mixing at all, such as large canids (Dorman and Bourne, 2010), or are incompatible due to similar niche occupancy (particularly noticeable amongst primates) (Buchanan-Smith, 2012). Kleiman *et al.*, (2010) suggests the benefits that mixing species of significantly different niches (e.g., an arboreal and a terrestrial species) can have in reducing interspecific competition for similar resources and thus, any conflict that may subsequently arise. In Dudley Zoological Gardens, UK, a potential case of incompatible mixing involving Patagonian mara (*Dolichotis patagonum*) and parma wallaby (*Macropus parma*) led to an increase in agonistic interactions and adaptation of enclosure usage for avoidance of one-another (Rendle *et al.*, 2018). Often, behavioural impasses regarding competition for resources are the cause of such issues, and present frequent challenges for zoo veterinarians (Kaandorp, 2012). Naturally associating species (i.e., those which would appear together in the wild) have proven to be the most compatible when it comes to co-existing (Buchanan-Smith, 2012).

1.2. *Capybara (Hydrochoerus hydrochaeris) habitat selection and sociality*

Rodents (Order *Rodentia*) are a group of mammals that have been kept in captivity by humans for centuries (Brandão & Mayer, 2011). The largest extant rodent species, the capybara (*Hydrochoerus hydrochaeris*), is recognised by many for its widespread distribution, unyielding social bonds, a high reproductive output and generalist grassland diet (Moreira and Macdonald, 1996). Across central South America, capybaras can be found in subtropical wetlands, marshes and swamps characterised by a variety of grasses and herbaceous plants (Schivo *et al.*, 2015). As a semi-aquatic mammal, free-ranging capybaras consider both the distribution and abundance of water bodies and surrounding vegetation in an area before selecting those to occupy (Corriale and Herrera, 2014). The importance of which stems from the species making frequent use of water bodies for mating, body temperature regulation and as a method of escaping terrestrial predators (Lord, 1994), a habit evidently maintained whilst held in captivity (Nogueira *et al.*, 2004). The majority of large South American herbivores such as the capybara, lowland tapir (*Tapirus terrestris*) and marsh deer (*Blastocerus dichotomus*) are linked by their foraging patterns and subsequent ability to modify terrestrial and aquatic ecosystems (Bakker *et al.*, 2016). Being a habitat generalist, capybaras are widespread within the Brazilian Pantanal, and often exploit similar resources to other generalists, particularly; deer (*Cervidae*), armadillo (*Dasypodidae*), porcupine (*Erethizontidae*) and tapir (*Tapiridae*) (Tomas *et al.*, 2010).

Sociality is a staple in capybara behaviour and underlies a fundamental part of the species' group dynamic, as capybaras often rely on other members of their group for survival (e.g., when being vigilant of predators) (Yáber and Herrera, 1994). In both wild and captive populations, capybaras strictly adhere to a well-established social structure amongst groups, which individuals often demonstrate by their desire to be pro-social towards subordinate group members when given the opportunity (Lalot *et al.*, 2021). Although it seems that the social structure within groups would be rarely challenged, it has been made apparent that social relationships between individuals in captivity are predominantly predicted by space availability (Nogueira-Filho *et al.*, 2017). By contrast, capybaras living in the wild do not appear to be governed by such limitations (with ranges up to 200ha in the Brazilian Pantanal) and have often been observed incorporating only minor increases in their territory size as their group expands (Herrera *et al.*, 2011). Thus, ensuring sufficient space relative to each individual's needs may be the key to success if capybaras are to maintain stable group bonds and additionally, to co-exist alongside other species successfully in captivity.

1.3. *The capybara as a specimen for mixed-species enclosures*

It is not unprecedented for capybaras to be kept in MSEs whilst held in captivity, the success of which Dortmund Zoo, Germany, have demonstrated with their South American mammal exhibit (including giant anteater (*Myrmecophaga tridactyla*) and lowland tapir) for over 40 years (Bartmann, 1980). A common theme amongst collections containing MSEs appears to be representative of distinct, native regions or habitats, consistent with perception preferences of both keepers and visitors alike (Green *et al.*, 2022). With respect to capybaras, one would expect to see MSEs corresponding with the continent of South America, grassland, and large water bodies. History has presented captive capybaras living alongside species with which they would naturally exist with in the wild, such as; spider monkey (*Ateles fusciceps*; Jens *et al.*, 2012), lowland tapir (Williams *et al.*, 2023), lesser rhea (*Rhea pennata*; Green *et al.*, 2022) and even Californian sealion (*Zalophus californianus*; Crotty, 1981). Despite a vast history of co-habitation (both *in-situ* and *ex-situ*) with other species, heterospecific

relationships (with the exception of parasite removal; Tomazzoni *et al.*, 2005; Sazima, 2007) between capybaras and other taxa are scarcely documented. Zoological literature also lacks an in-depth examination of how capybaras behave with respect to a variety of South American species, and the potential for confinement to infringe on captive’s welfare if suitable pairings are not established. It is important to note that captive-born capybaras behave distinctively to that of their wild-born conspecifics, particularly in relation to enclosure usage and predator vigilance (Nogueira *et al.*, 2004). Such behavioural differences could provide explanation for potential heterogeneity amongst the rate at which captive groups assimilate into a variety of MSEs, a topic in dire need of further investigation.

1.4. Study aims

The aim of this study is to investigate the behavioural implications of a mixed-species captive setting on groups of capybaras housed at Blackpool Zoo, UK. Specifically, this study will focus on the influence of enclosure habitat composition and the presence of co-habitant partner species to which the capybaras share their enclosure with. The extent to which these factors determine the overall behaviour of capybaras will be assessed using scan-sampling observations of individual’s behaviour, relating it to their location within the enclosure, as well as proximity to the partner species. Findings will be used in conjunction with scientific literature to deduce if the current enclosure settings are suitable for the capybaras. Precisely, this study aims to establish which partner species is the most suitable, and which (if any) has the potential to compromise the welfare of the capybaras. Location selection within the enclosure and how this may differ between groups will also be considered, as well as any potential behavioural ramifications.

2. Materials and Methods

2.1. Study site

This study was carried out at Blackpool Zoo, UK (53.8159° N, 3.0104° W), and centred around observing the behaviour and interactions of 13 resident capybaras ($n = 13$). The capybaras studied comprised three separate groups – Enclosures A, B and C (**Table 1**). Each enclosure was a mixed-species exhibit and aside from group composition, was distinct in two respects, (1) habitat types and (2) partner species occupying the enclosure, alongside the capybaras.

Table 1 – Group composition, habitat type and partner species within enclosures

Enclosure	Dominant habitat	No. of individuals	Sex	Partner species
A	Lake	3	Female	Spider monkey (<i>Ateles fusciceps robustus</i>), Pileated gibbon (<i>Hylobates pileatus</i>)
B	Woodland	3	Male	Lowland tapir (<i>Tapirus terrestris</i>)
C	Grassland	7	Mixed	Giant anteater (<i>Myrmecophaga tridactyla</i>), Patagonian mara (<i>Dolichotis patagonum</i>)

The dominant habitat type in enclosure A is water (1 in **Figure 1**) in the form of a lake (area = 1,752.53m²; perimeter = 162.83m), which makes up a vast expanse in the centre of the enclosure. The enclosure encompasses substantial grassland (2 in **Figure 1**) surrounding the perimeter of the lake, and an indoor house (3 in **Figure 1**) at the south-east corner. The area directly in front of the indoor house contains feeding troughs (also 3 in **Figure 1**), where the capybaras are routinely fed each day. Two islands (5 in **Figure 1**) lying parallel to one another can be observed in the centre of the lake. These islands are where the partner species (pileated gibbon and spider monkey) can be seen regularly socialising. Zoo visitors can observe the animals from the perimeter fence running alongside the north, west and south-west edges of the enclosure (**Figure 2**). The observer was stationed along a mud track running alongside the east perimeter fence.

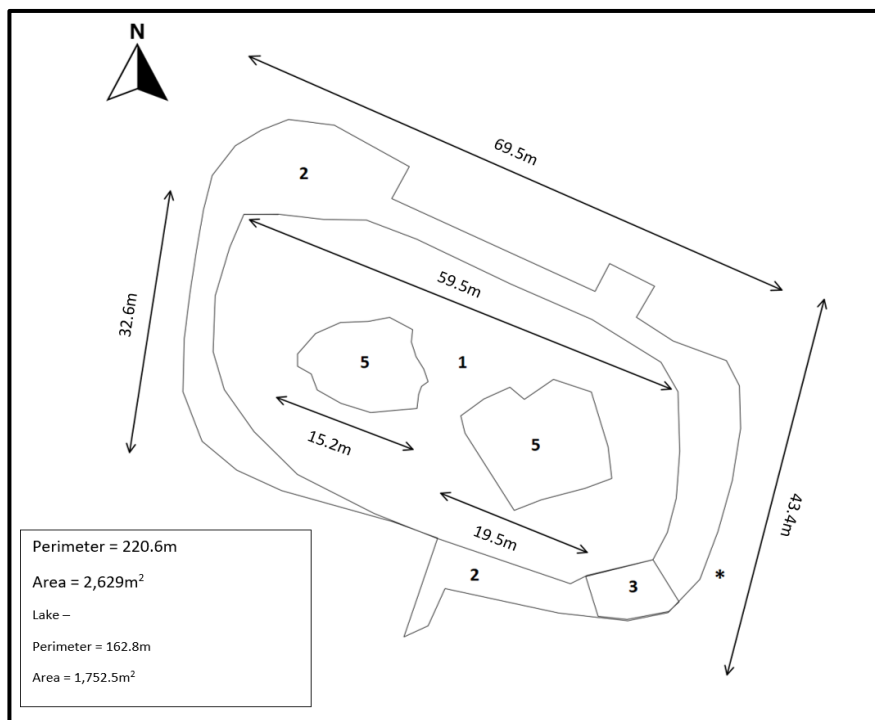


Figure 1 – Enclosure A. Water (1), grassland (2), indoor house & feeding troughs (3), stone patch (5). *Observer location



Figure 2 – Enclosure A. Views from the north-west (1), south-west (2) and north (3) perimeter fence

The dominant habitat type in enclosure B is woodland (4 in **Figure 3**) (area = 1,216.81m²; perimeter = 151.79m), which extends throughout the enclosure with the exception of the north-west (NW) corner and a section of outbuild to the west. The water (1 in **Figure 3**) constituting the pool and a stone patch (5 in **Figure 3**) lie to the NW, with the indoor house and feeding troughs (3 in **Figure 3**) accounting for the area to the far west. Separate feeding troughs (also 3 in **Figure 3**) are also situated to the west, approximately 12m east from the indoor house, and are the location of routine feeds during the daytime. A viewing platform runs parallel to the enclosure along the south perimeter and on a steep embankment. Zoo visitors can observe the animals from anywhere along the fenced perimeter, except for a 29.82m stretch from the indoor house to the west-end of the viewing platform (**Figure 4**). The observer was stationed at the west end of the viewing platform along the south perimeter fence.

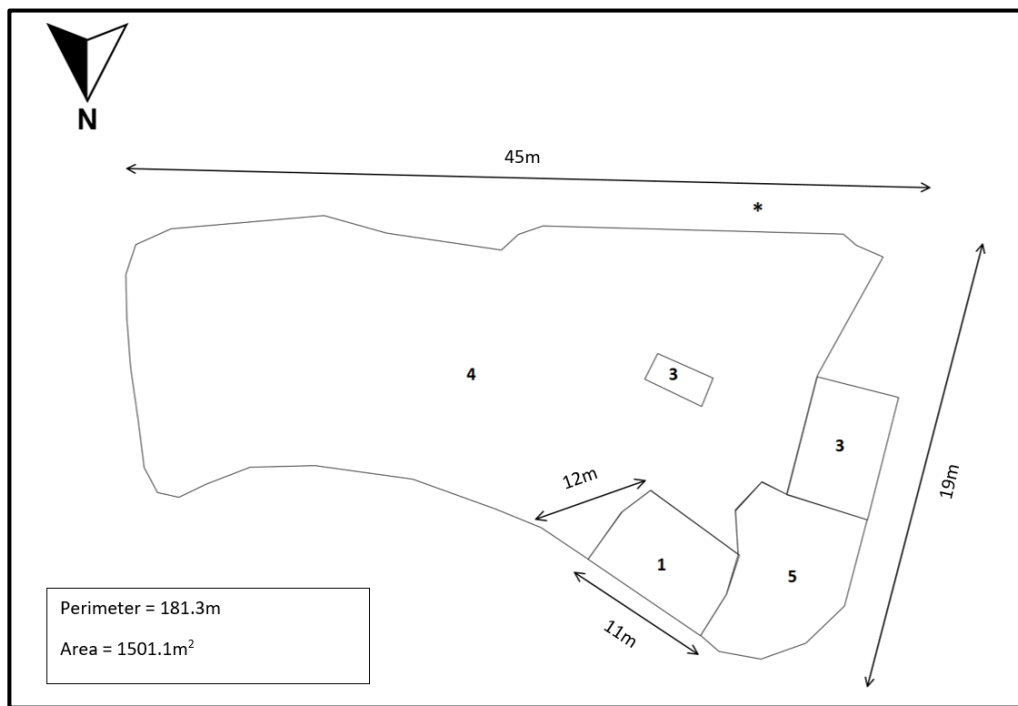


Figure 3 – Enclosure B. Water (1), indoor house & feeding troughs (3), woodland (4), stone patch (5). *Observer location



Figure 4 – Enclosure B. Views from the north (1), south embankment (2) and south-west (3) perimeter fence

Enclosure C is mainly dominated by grassland (2 in **Figure 5**) (area = 876.09m²; perimeter = 103.07m), with a large section of land shadowed by overhanging trees residing to the north and denoted as woodland (4 in **Figure 5**). The water (1 in **Figure 5**) constituting the pool lies to the south, with an indoor house (3 in **Figure 5**) situated to the west and a shelter with feeding troughs (also 3 in **Figure 5**) roughly centred. During the day, the capybaras in enclosure C are scatter fed on the grassland, with food also being distributed in the feeding troughs. Zoo visitors can observe the animals in enclosure C from the perimeter fence facing south and east only (**Figure 6**). Due to the nature of the enclosure, the observer utilized two locations for observations – along both the south and east perimeter fence.

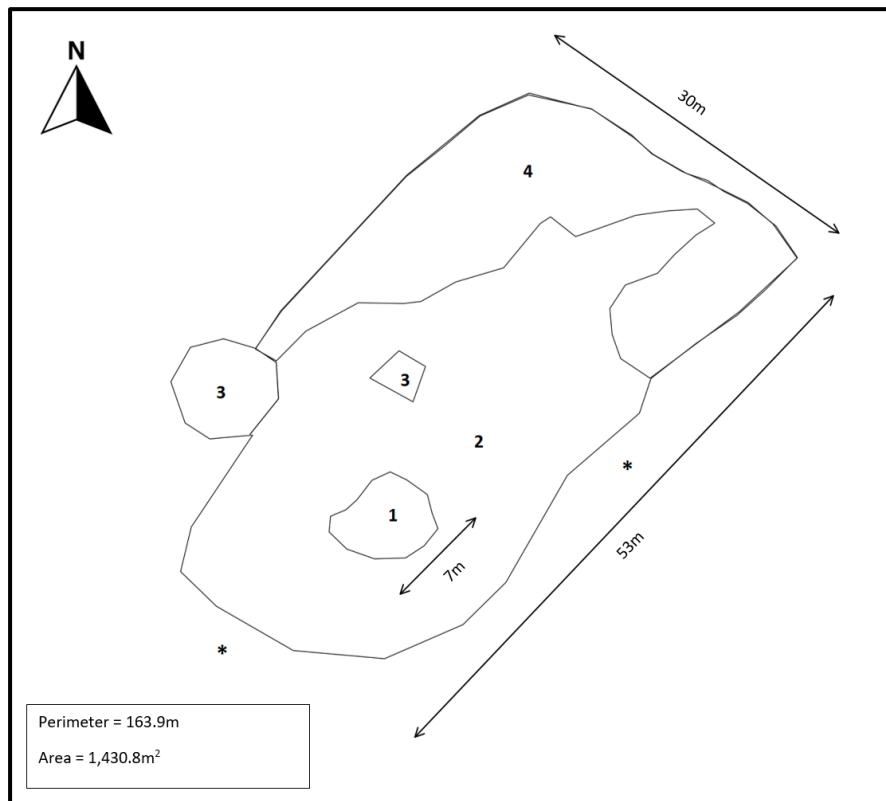


Figure 5 – Enclosure C. Water (1), grassland (2), indoor house & feeding troughs (3), woodland (4). *Observer location



Figure 6 – Enclosure C. Views from the south-east (1), east (2) and south (3) perimeter fence

2.2. Data collection

The study period ran for a total of 12 weeks, and consisted of four observation sessions per group, per week, from 04/10/2022 until 21/12/2022 (336 observations to be taken per individual). Two observation sessions were conducted per day, one in the morning and one in the afternoon (repeated for each enclosure). Observation sessions lasted for 30 minutes, with observations taken every five minutes (time interval sampling: Bateson and Martin, 2021).

Behavioural observations were taken using a scan-sampling technique (Bateson and Martin, 2021), as each individual was identified within the enclosure and details of their behaviour and chosen location at the time were noted. A third variable was measured at each observation, i.e., proximity (m) of each individual to the nearest member of the partner species in that enclosure. The purpose of measuring changes in proximities was to isolate any behavioural patterns that existed in relation to the partner's species and their specific behaviour, to which the capybaras were consistently subjected to.

Individual capybaras were identified using ID sheets (**Appendix 1**), which contained images and a list of features that enabled the observer to tell each individual apart. The behaviour of capybaras was recorded using an ethogram (**Appendix 2**), and was categorised into either socio-positive, socio-negative, feeding, grooming, active or inactive. The location at which each individual resided in during observations was recorded using enclosure schematics (**Figure 1**, **Figure 3** and **Figure 5**), and was divided into water, grassland, indoor house and feeding troughs, woodland or stone patch. The proximity between each capybara and the nearest member of their partner species was measured using estimates obtained from the same enclosure schematics used to allocate location data, which contained dimensions of all the main features of the enclosures. Any interactions that occurred between any capybara and a member of a partner species was noted, as well as any external factors that may affect any of the variables being measured. Such factors included many unavoidable stimuli and ranged from feeding sessions to establishing enrichment to construction noise from nearby enclosures.

2.3. Data analysis

To analyse behavioural data, each individual observation was treated as an independent sample. Initial exploratory tests were used to determine if an autocorrelation existed between dependent variables (i.e., behaviour, location and proximity). A Chi-squared (X^2) test of association was used for nominal data, i.e. location *versus* behaviour and a Kruskal-Wallis, non-parametric test was used for continuous data, i.e. to test location *versus* proximity and behaviour *versus* proximity. Post-hoc Dunn's tests were used to identify where significant differences occurred. Kruskal-Wallis (and associated Dunn's test) also enabled the observer to investigate the extent to which partner species influenced the proximity between the capybaras and the nearest member of their partner species. Similarly, an additional Chi-squared (X^2) test was used to determine if the partner species effected the capybara behaviour. All tests were used with a statistical significance threshold set to $p = 0.05$. Chi-squared (X^2) tests were performed by hand using a contingency table (**Appendix 3a**, **3b** and **3c**), with all other tests calculated using RStudio (version 2021.09.0) statistics software (**Appendix 4a**, **4b** and **4c**).

3. Results

3.1. Overview

A total of 2,139 observations were finalised for this study (enclosure A = 458; enclosure B = 281; enclosure C = 1400; **Appendix 5a, 5b** and **5c**). 97 “out of sight” observations were documented (enclosure A = 26; enclosure B = 56; enclosure C = 15), where capybaras (or the partner species) were not in sight and data was not recorded. Finalised data did not include any “out of sight” observations. Sample sizes differed substantially between enclosures due to differences in group size (**Table 1**) and other unavoidable scenarios that hindered the data collection process.

3.2. Tests for autocorrelation

3.2.1. Behaviour & location

During observations, each capybara’s chosen location was significantly associated with their behaviour at that time ($X^2 = 92.87$, $df = 20$, $p < 0.001$). As behaviour was the focus of this investigation, location was omitted from subsequent analysis as its association with behaviour made analysing both variables separately redundant (i.e., capybaras would consistently perform a certain behaviour in a particular location).

3.2.2. Proximity effects on behaviour & location

Each capybara’s location was independent to their proximity to the nearest partner species ($t = 89.26$, $df = 4$, $p < 0.001$). Likewise, capybara behaviour was independent to the proximity of the nearest partner species ($t = 19.92$, $df = 5$, $p < 0.001$). Post-hoc tests revealed six and one significant result(s) accounting for differences between proximity measurements for a combination of locations (**Table 2**) and behaviours (**Table 3**) respectively.

Table 2 – Results of post-hoc Dunn’s test (Proximity versus location)

Location 1	Location 2	p-value	Interpretation
Indoor	Stone	0.096	<i>No Significance</i>
Indoor	Water	0.039	<i>Significant Difference</i>
Indoor	Woodland	< 0.001	<i>Significant Difference</i>
Indoor	Grassland	< 0.001	<i>Significant Difference</i>
Grassland	Stone	< 0.001	<i>Significant Difference</i>
Grassland	Water	0.495	<i>No Significance</i>
Grassland	Woodland	0.478	<i>No Significance</i>
Water	Stone	0.003	<i>Significant Difference</i>
Water	Woodland	0.495	<i>No Significance</i>
Woodland	Stone	< 0.001	<i>Significant Difference</i>

Table 3 – Results of post-hoc Dunn’s test (Proximity versus behaviour)

Behaviour 1	Behaviour 2	p-value	Interpretation
Inactive	Feeding	0.014	<i>Significant Difference</i>
Active	Feeding	0.427	<i>No Significance</i>
Active	Grooming	1	<i>No Significance</i>
Active	Inactive	1	<i>No Significance</i>
Active	Socio-Negative	0.427	<i>No Significance</i>
Active	Socio-Positive	0.338	<i>No Significance</i>

Feeding	Grooming	1	No Significance
Feeding	Socio-Negative	1	No Significance
Feeding	Socio-Positive	0.735	No Significance
Grooming	Inactive	1	No Significance
Grooming	Socio-Negative	1	No Significance
Grooming	Socio-Positive	1	No Significance
Inactive	Socio-Negative	0.461	No Significance
Inactive	Socio-Positive	0.427	No Significance
Socio-Negative	Socio-Positive	1	No Significance

3.3. Location selection

Overall, the largest proportion of location observations (for the three enclosures combined) came from grassland ($n = 979$; 45.77%) followed by indoor & feeding area ($n = 899$; 42.03%), with substantially less recorded for woodland ($n = 223$; 10.43%), for water ($n = 18$; 0.84%) and for stone patch ($n = 20$; 0.94%). A similar trend in location selection was observed within each enclosure (**Figure 7**), except for enclosure B (Note: enclosure B does not contain any grassland, enclosure A any woodland or enclosure C any stone patch). The highest relative proportion of grassland observations came from enclosure C (56.79%) where grassland dominates. Similarly, woodland was selected for most in enclosure B (71.17%) where woodland dominates. In enclosure A, a very little proportion of water (dominant habitat) observations were recorded (1.75%), which was also apparent in enclosures B (1.07%) and C (0.5%). The capybaras in enclosure B selected the stone patch more than those in enclosure A (7.12% and 0% respectively).

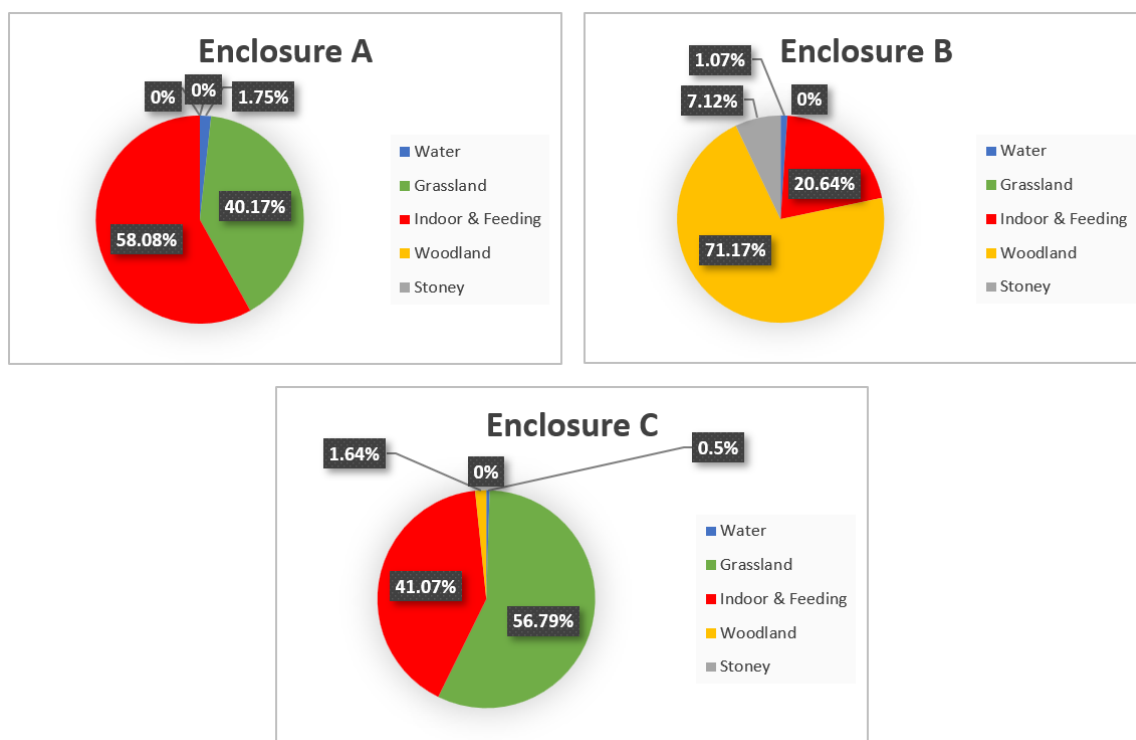


Figure 7 – Proportion of selected locations within enclosures

3.4. Proximity & partner species

Across the three enclosures, measured proximities between capybaras and their partner species were independent to the species present at that time ($t = 674.63$, $df = 4$, $p < 0.001$) (**Figure 8**). On average, proximity was furthest between capybaras and the spider monkey ($23.5\text{m} \pm 9.03$) and pileated gibbon ($23.4\text{m} \pm 9.11$), which noticeably reduced to the lowland tapir ($13.4\text{m} \pm 11.93$) and giant anteater ($8.2\text{m} \pm 7.55$), with the shortest average existing between the capybaras and the Patagonian mara ($7.9\text{m} \pm 7.42$). Despite these results, differences in sample sizes for each partner species were substantial; giant anteater ($n = 10$), pileated gibbon ($n = 291$), Patagonian mara ($n = 1390$), spider monkey ($n = 167$), lowland tapir ($n = 281$) and must be considered when interpreting these significances. Post-hoc tests identified eight significant results between overall proximities for a combination of partner species (**Table 4**).

Table 4 – Results of post-hoc Dunn’s tests (Proximity versus partner species)

Species 1	Species 2	p-value	Interpretation
Anteater	Tapir	0.831	No Significance
Anteater	Mara	0.831	No Significance
Anteater	Monkey	< 0.001	Significant Difference
Anteater	Gibbon	0.005	Significant Difference
Gibbon	Mara	< 0.001	Significant Difference
Gibbon	Monkey	< 0.001	Significant Difference
Gibbon	Tapir	< 0.001	Significant Difference
Mara	Monkey	< 0.001	Significant Difference
Mara	Tapir	< 0.001	Significant Difference
Monkey	Tapir	< 0.001	Significant Difference

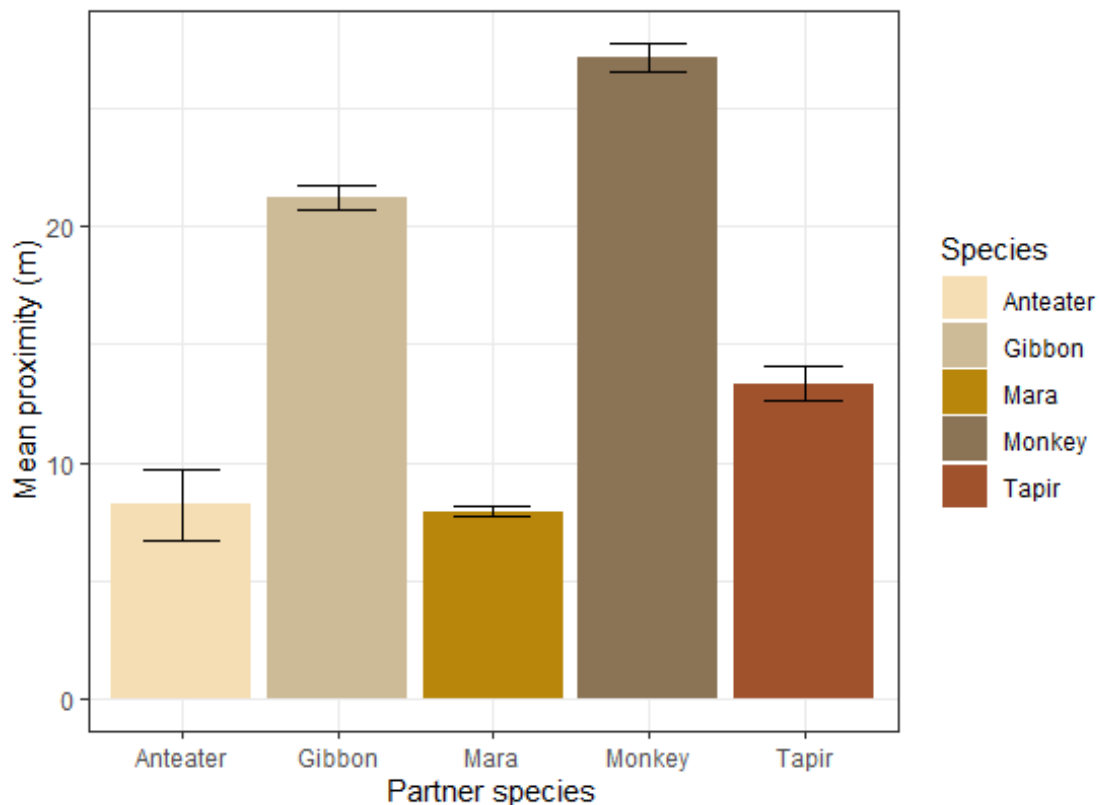


Figure 8 – Mean proximity (m) observed between capybaras and partner species (giant anteater, pileated gibbon, Patagonian mara, spider monkey and lowland tapir)

3.5. Behaviour & partner species

Capybara behaviour, when exhibited, was significantly different in the presence of each partner species within closest proximity ($X^2 = 127.21$, $df = 20$, $p < 0.001$) (**Figure 9**). Such a difference remained even after the giant anteater (partner species with the lowest sample size; $n = 10$) observations had been removed ($X^2 = 87.53$, $df = 15$, $p < 0.001$). Some patterns of behaviour observed were similar in the presence of all species, with inactive (39.69% of all observations) and feeding (53.76% of all observations) dominating recorded behaviours (except in the presence of the giant anteater). The relative proportion of active capybaras (4.35% of all observations) was highest in the presence of the giant anteater (40%) and in similar proportions near all other species – pileated gibbon (4.12%), Patagonian mara (3.81%), spider monkey (1.80%) and lowland tapir (7.47%). Socio-positive interactions (0.33% of all observations) were only observed in enclosures B and C in the presence of the Patagonian mara (0.43%) and the lowland tapir (0.36%). Conversely, socio-negative interactions (0.84% of all observations) were observed in all enclosures within proximity to the Patagonian mara (1.08%), spider monkey (1.2%) and the lowland tapir (0.36%). Grooming behaviour (1.03% of all observations) was also relatively absent during observations, despite being observed in the presence of all partner species (in very low frequencies); giant anteater (0.05%), pileated gibbon (0.05%), Patagonian mara (0.75%), spider monkey (0.05%), lowland tapir (0.14%).

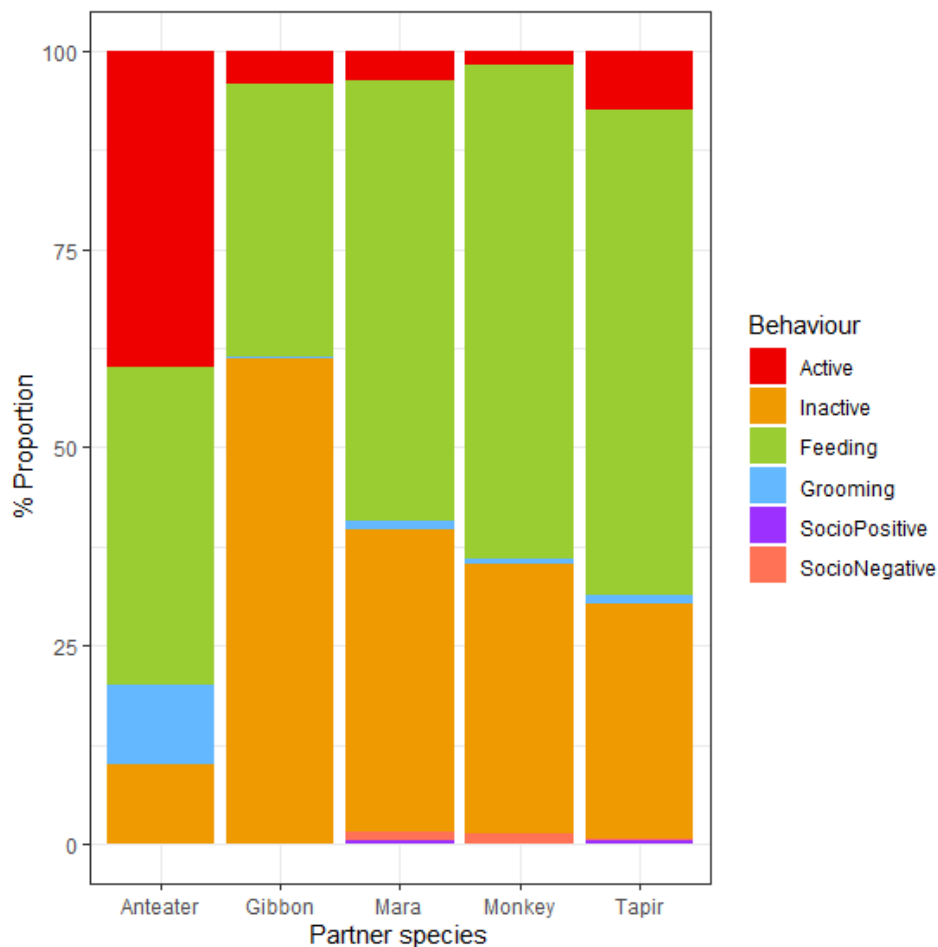


Figure 9 – Proportion of behaviours (active, inactive, feeding, grooming, socio-positive and socio-negative) observed in the presence of partner species (giant anteater, pileated gibbon, Patagonian mara, spider monkey and lowland tapir)

4. Discussion

4.1. *Capybaras within a MSE*

4.1.1. *Overview*

The behaviour and location of capybaras in this study were affected by enclosure, more specifically, the partner species. Despite this, similarities (in both proportion and frequency) of behaviours and locations were observed in the presence of all partner species, suggesting that the significant effect observed is likely due to extremely varied sample sizes across species. Proximity was used as an indicator for the strength and directionality of relationships between capybaras and each partner species. However, the lack of effect proximity had on the capybara's behaviour leaves some questions unanswered. That is, if proximity does not mediate the associations found in this study, what other present factor(s) could be responsible. Free-ranging capybaras in the Brazilian Pantanal have been observed exhibiting low vigilance levels when proximity to potential predators remains high, despite the constant threat of such predators in the surrounding area (Avila *et al.*, 2022). Similarly, capybaras will naturally modify their habitat usage (including extending and restricting their range) to distance themselves from the threat of perceived danger (Lopes *et al.*, 2021). Hence, the concept that capybara behaviour is influenced by proximity to other species remains valid. In this study, a high proximity between capybaras and certain species remains a likely indicator of a capybara's selectivity to occupy locations where they feel safer, although further research is required to corroborate this. Similar studies on capybara behaviour within a MSE, including recently by Williams *et al.*, (2023), fail to acknowledge how the group may be influenced behaviourally by the partner species present.

4.1.2. *Observed behaviour and location selection*

There is solid evidence to suggest that the capybara gut is well adapted to a diet composed of grasses (Ferreira *et al.*, 2012; Kiani *et al.*, 2018). In the wild, capybaras forage by actively selecting those plants that are high in energy and nutritional value (Corriale *et al.*, 2011), and that can be found in a wide range of native grassland (Herrera *et al.*, 2011). Therefore, it is not surprising that given a choice, grassland dominated the location selection for the capybaras in this study, likewise for feeding amongst behaviours. The absence of capybara sightings in the water, particularly in enclosure A (of which comprises approximately two-thirds of the enclosure) raises some questions given the species' dependence on water for reproduction (Alvarez and Kravetz, 2005), in addition to thermoregulation and as a source of nutrition (Herrera and Macdonald, 1989). Captive capybara studies have also denoted water bodies within an enclosure as a vital "safety blanket" during times when individuals feel threatened (Nogueira *et al.*, 2004). It is inevitable that by entering the water, individuals in enclosure A are reducing their proximity to the partner species, and the idea of avoiding danger by maintaining a large distance reinforces the pattern of location selection observed. The little observations acquired from other groups may correspond to the small area of the pool (15.7m²/1.1% of enclosure area) in enclosure C or perhaps the use of the pool by the tapirs in enclosure B (1.07% of all enclosure B observations; 13.4m ± 11.93 average proximity may suggest reluctance to associate) of which could affect the capybara's use of it. Socio-positive behaviour is undoubtedly a marker for stable

social relationships amongst capybaras. Lalot *et al.*, (2021) demonstrated that pro-sociality in capybaras is largely determined by sex, with females on average choosing to reward conspecifics more often than males. Interestingly, socio-positive interactions were only observed in enclosures B and C (all male and mixed groups), with no such interactions exhibited within enclosure A (all female group). By contrast, socio-negative interactions were observed in enclosure A (all female group), albeit at a low proportion (1.2% of all observations). Supporting evidence and findings from this report would suggest that females in enclosure A could be exhibiting behavioural deviances due to co-habitation with their partner species.

4.1.3. Evaluation of partner species'

At Blackpool Zoo, the primates (pileated gibbon and spider monkey) in enclosure A are consistently furthest from the capybaras ($23.4\text{m} \pm 9.11$ and $23.5\text{m} \pm 9.03$ average proximity, respectively) out of the five partner species studied. Interestingly, records from Apenheul Primate Park, Netherlands, describe capybaras as a successful cohabitant to spider monkeys during trials of a new mixed-species exhibit during the 1970's (Jens *et al.*, 2012). A large part of this success is down to the species occupying two completely separate niches (i.e., arboreal vs grazer) in addition to ample space (area = $2,629\text{m}^2$ in this study) to take advantage of, distanced from one-another (Probst and Matschei, 2008). Again, this leaves uncertainty as to whether proximity is a true indicator of capybara interspecific relationships. According to observations, the Patagonian mara is consistently the closest out of those species that capybaras at Blackpool Zoo reside with ($7.9\text{m} \pm 7.42$ average proximity to capybaras). Interestingly, the two species do not share similar social living in the wild (Tomas *et al.*, 2010), with maras historically existing as monogamous pairs during the majority of their lives. However, both species have adopted similar distribution patterns largely predicted by the abundance and distribution of vegetation. Research suggests that larger social groups of both intra- and interspecific composition are more common amongst *Caviomorpha* (including both capybara and mara) when resources are abundant within a habitat of high homogeneity (Macdonald *et al.*, 2007). The abundance and distribution of food, to which both species rely on, within enclosure C as scatter feeds and within troughs may enable a willingness to exist within close proximity to one-another as a larger social group. A minute proportion of giant anteater observations (0.47% of all enclosure C observations) does not provide enough indication as to how capybaras behave in their presence, although established MSEs suggest the two species co-habit successfully (Bartmann, 1980). With the exception of relatively absent pool observations (1.07% of all enclosure B observations), capybaras in enclosure B appear to maintain a noticeable distance ($13.4\text{m} \pm 11.93$ average proximity) between themselves and the lowland tapir. Williams *et al.*, (2023) reports that both capybara and tapir of a MSE adopt similar behaviours to one-another in response to stimuli originating near their paddock. The extent to which the behaviours are interspecifically linked between individuals is lacking.

4.2. Recommendations

Findings from this report do not provide adequate justification to consider a change in the captive setting of capybaras at Blackpool Zoo. However, capybaras in enclosure A may require further evaluation to explain some deviations in both behaviour and enclosure usage. Firstly, a consistently larger proximity to their partner species could indicate an ongoing selectivity to remain in locations where they feel safe. Given the significant impression that partner species had on capybara behaviour (and location), the possibility that the capybaras are modifying their behaviour in response to the

primates remains. Second, a lack of observations taken where individuals occupied the water in the enclosure could be a cause for concern. The lake in enclosure A comprises 66.7% of the entire enclosure. Only 1.8% of observations were taken from capybaras in the water, which may further give reasoning for reluctance to adapt their behaviour (and possibly reduce the proximity to the partner species) in response to potential threats, or perhaps other external factors may influence the capybara's decision to enter the lake. Based on findings from this report, it is recommended that further research is conducted on potential reasons why capybaras would want to avoid the primates (at Blackpool Zoo specifically). Separate to this, it is recommended that an extension into how capybaras in enclosures B and C use their water features is implemented. A lack of observations (as previously mentioned) may indicate that the pools are not sufficient, given their relatively small size (in relation to the enclosures) for capybaras to maintain a comfortable distance between themselves and the partner species. A long-term extension of this study may provide enough evidence to prove this or suggest otherwise.

4.3. Further investigation

A drawback of this study is the inability to specifically deduce a preference *per se* of partner species by the capybaras. As individuals were not provided with equal exposure to all partner species during observations, likely comparisons cannot be made as to how all capybaras would behave in respect to each species given the opportunity. In order to enhance the findings here, further investigation involving a capybara group exposed to several species of a range of ecological niches (e.g., primates and maras) would supply zookeepers with the optimal methods to conclude how the species responds to each.

Given that the capybaras at Blackpool are to some extent separated by sex, an obvious extension of this study would include examining sexual differences in behaviour and enclosure usage. With respect to sociality and space utilisation, wild capybaras have demonstrated significant behavioural dissimilarity between males and females in terms of scent-marking (Macdonald *et al.*, 1984), pro-sociality (Lalot *et al.*, 2021) and perhaps most importantly, distribution patterns (Congdon, 2007). There is however little insight into how these sexual differences would transpire in a captive (specifically a MSE) setting, with respect to other taxa. The findings of such an extension may provide a critical take on how individuality may influence the response to a selection of partner species and assist zookeepers at Blackpool Zoo in improving the captive setting of their capybara collection.

4.4. Final thoughts

The question as to whether captive capybaras housed at a UK zoo are affected by a MSE environment is true to some extent. Specifically, this study has indicated that the partner species has some effect on their behaviour and subsequently location within the enclosure. However, the proportion of behaviours exhibited showed substantial similarity, incurring the possibility that the effect of the partner species on capybara behaviour is due to sample size differences. Proximity between the species has not proved to be a clear factor in affecting capybara behaviour, although it cannot be ruled out due to contradictory literature and heterogeneity amongst groups. Therefore, there is little evidence to justify considering changing the MSE setting of capybaras at Blackpool Zoo for improving welfare. More research is needed to deduce how the interspecific relationships involving capybaras in captivity transpire, and what factors may contribute to a change in behaviour.

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