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The behavioural response of captive *M. nigra* and *C. capucinus* to a novel cooperative enrichment device at Newquay Zoo

by

Julia Ann Sullivan

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Author’s Declaration

At no time during the registration for the degree of Research Masters has the author been registered for any other University award, without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

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Abstract

In the wild, primates cooperate to overcome challenges and maximise survival. Introducing cooperative tasks to zoo-housed primates may enhance welfare and promote prosocial behaviour in a captive setting. Comparative research on primate cooperation has predominately taken place in primate research facilities, where they are able to control pairing of individuals and incorporate task specific training. Zoos offer the opportunity to explore cooperation under more naturalistic conditions, but there is limited existing literature. I investigated the cooperative behaviour of socially housed groups of Sulawesi black crested macaques (*Macaca nigra*) (n=7) and White-throated capuchins (*Cebus capucinus*) (n=4) at Newquay Zoo, using novel cooperative pulling tasks. I assessed the ability of the primates to cooperate without prior training, the group of *M. nigra* were unable to solve the cooperative task to gain a food reward, in the group of *C. capucinus* the dominant male was able to obtain the food reward using an alternative strategy. I conducted behavioural observations using focal scan sampling to assess the activity budgets of subjects comparing behaviour when the cooperative enrichment device was present (10 enrichment days) and when it was not (10 baseline days). I identified minimal differences in activity budgets between the two conditions, suggesting that there was no negative impact on welfare. Additionally, I investigated levels of interaction with the device. I predicted that approaches to, and interactions with, the device would decrease over the trials due to habituation. I found that interactions with the device varied among subjects, were higher in males and in both groups interaction with the device increased over the trials as did rope pulling actions, indicating that the device provided stimulation over the course of the study. In the *M. nigra* group, I compared the number of solitary and social rope-pulling actions, and found that subjects pulled the ropes more often in the presence of others. I conclude that cooperative devices and tasks that require spontaneous cooperation should continue to be explored in zoo settings and that this could be combined with training to encourage prosocial behaviours. In future studies, cooperative enrichment devices should be evaluated over more trials to further assess the appropriateness and welfare benefits of cooperative enrichment tasks in zoos.

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1. Introduction

1.1 Cooperation

Cooperation is defined as the act of individuals or groups working together towards a common goal or objective (Stephens and Anderson, 1997; Brosnan and Bshary, 2010). In this context, cooperation includes any behaviour that provides a benefit either to another individual (recipient) or is advantageous for both the individual performing the behaviour (actor) and the recipient (Brosnan and Bshary, 2010). Cooperation requires animals to help each other, examples exist across both human and non-human animals, and are considered widespread and multifarious (Schweinfurth and Call, 2019a).

Cooperation is a complex social behaviour, that continues to challenge research disciplines because of the multifaceted nature of cooperative behaviour (Henrich and Muthukrishna, 2021). Group living offers the advantage of cooperative behaviour, understanding how cooperation is maintained in relation to the distribution of costs and benefits associated with cooperative behaviour, is challenging (Williams, Shultz and Jensen, 2022). Evidence of cooperation has been documented across a range of taxa, with differing degrees of complexity. Studies have included among others, cooperative nesting behaviour of harvest ants (*Pogonomyrmex californicus)* (Haney and Fewell, 2018); cooperative predator inspections in wild guppies (*Poecilia reticulata*) (Croft *et al.*, 2006); cooperative rope pulling task, to access enrichment in bottlenose dolphins (*Tursiops truncates)* (Yamamoto *et al.*, 2019)*;* cooperative pulling tasks in Asian elephants *(Elephas maximus)* (Li *et al.*, 2021) and brown capuchin monkeys (*Cebus apella*) (Mendres and de Waal 2000). Research continues to investigate cooperative behaviour from both ultimate and proximate explanations (West, Griffin and Gardner, 2007). Ultimate explanations have examined the evolution of cooperation through kin selection and reciprocity, whilst proximate explanations have focused on investigating the cognitive mechanisms associated with cooperation (Mendres and de Waal, 2000).

Cooperation can result in either direct or indirect fitness benefits and is therefore a form of prosocial behaviour (Langergraber *et al.*, 2007). Group hunting in chimpanzees (*Pan troglodytes*), is an example of how an individual can gain direct nutritional fitness benefits through cooperative hunting behaviour (Boesch, Boesch and Vigilant, 2006). The cooperative breeding behaviour of Golden lion tamarins (*Leontopithecus rosalial*) is an example of indirect fitness benefits, where individuals indirectly benefit by caring for related infants (Henry *et al.*, 2013; Thornton and Mcauliffe, 2015). Whilst evidence of cooperative behaviour exists within a variety of species, research often focuses on humans and non-human primates when trying to answer complicated questions that challenge the theoretical concept of individual fitness (van Schaik and Kappeler, 2006) . Explanations of the evolution of cooperative behaviour continues to be a focus of scientific research with the aim of answering unresolved questions and deepening our knowledge (Langergraber *et al.*, 2007).

Cooperation as a fundamental aspect of social behaviour, falls within the social cognition framework as it requires individuals to be able to interpret and process social information, respond accordingly and take advantage of social environments (Frith, 2008; Byrne and Bates, 2010). For cooperation to be successful, actions need to be synchronised and coordinated (Range *et al.*, 2019). Cooperation is often associated with human societies as it involves high levels of cognitive and social complexity (Melis and Semmann, 2010; Duguid and Melis, 2020). However, cooperation is not unique to humans, and many species of animals engage in cooperative behaviour to varying degrees (Melis and Semmann, 2010). Levels of cooperation seen in animals can range from a by-product of uncoordinated actions, simple coordinated activities to complex social behaviours that require high levels of communication, coordination and collaboration (Duguid and Melis, 2020; Petit, Desportes & Thierry, 1992). Albiach-Serrano (2015) reviewed Boesch and Boesch (1989) categories of cooperation and how actions can be influenced by others; table 1 outlines the operational definitions of cooperation categories, categories 2-5 clearly define the impact of others' on individual's actions.

Table 1: Operational definitions of cooperation categories. (modified from Albiach-Serrano, 2015, excluding correspondence to Boesch and Boesch 1989).

	Category	**Definition**
1	Independent cooperation	Individuals perform actions independently (i.e., without adjusting to each other)
2	Presence-dependent cooperation	Individuals are more likely to act in the others' presence
3	Action-dependent cooperation	Individuals are more likely to act when the others perform a particular action
4	Form-dependent cooperation	Individuals adjust their actions to those of others in time, space or both
5	Intentional cooperation	Individuals attend to others' actions and choose accordingly and flexibly the type of action to perform as a result of understanding the others' role in solving the problem

Cooperation facilitates important social bonds by reducing agonistic behaviour, aiding conflict resolution, facilitating cooperative breeding and defending and protecting resources and territories (West *et al.,* 2007). Establishing explanations for cooperative behaviour continues to be a focus of interest in animal behaviour and evolutionary biological research because cooperation raises several unanswered questions, surrounding explanatory mechanisms, theories of competition, individual fitness and natural selection (Gokcekus *et al.*, 2021).

Cooperation is considered fundamental in non-human primate societies (Schmelz & Call 2016). Across many primate species, individuals invest in prosocial behaviour, with cooperation being a crucial aspect associated with the maintenance of social bonds (Berghänel *et al.,* 2011). Examples of primate cooperation observed in the wild, include the cooperative breeding in callitrichids, where non-parent individuals help care for the offspring of others, this behaviour is associated with high level cognitive performance and prosociality (Burkart and van Schaik, 2010). A second example of primate cooperation is coordinated intergroup gang attacks observed in wild *M. nigra* (Martínez-Íñigo *et al.*, 2021). Martínez-Íñigo *et al.,* (2021), propose that to evaluate the cognitive skills and mechanisms related to this behaviour, further investigation is needed to determine whether gang attacks are pre-planned or whether they are simply reactive aggressive behaviour. Micheletta *et al.*, (2012) also provide evidence of cooperative behaviour in wild *M. nigra.* Their research suggests that successful cooperative defence against predators is associated with strong social bonds in this socially tolerant specie (Micheletta *et al.*, 2012). What is evident is that cooperative, collaborative behaviour is evident in *M. nigra* in the wild. A third example is the cooperative rescue of a juvenile white-faced capuchin (*Cebus imitator*) from a boa constrictor attack (Jack *et al.*, 2020). The alpha male, alpha female and the juveniles mother, all attacked the boa constrictor and rescued the juvenile, whilst other group members engaged in vocal mobbing. This observation provides evidence of cooperative group behaviour and its importance in predator defence (Jack *et al.*, 2020).

Researching cooperation in non-human primates can be challenging, due to complex social dynamics and the varying cognitive abilities of different species (Kershenbaum and Blumstein, 2017). Some of the main challenges of researching and explaining cooperative behaviour include:

1. Determining the motivation for cooperation: Understanding the motivation behind cooperative behaviour can be difficult as it may vary depending on the species and the situation (Schmelz and Call, 2016; Williams, Shultz and Jensen, 2022). For example, some primates may cooperate for mutual benefits, while others may do so to gain social status or to reduce conflict within a group.
2. Accounting for individual variation: Cooperative behaviour can vary widely among individuals within a species, and factors such as age, sex, and social status can influence the likelihood of an individual engaging in cooperative behaviour (Flack *et al.*, 2006; Williams, Shultz and Jensen, 2022). Accounting for this individual variation can be challenging, as it requires detailed observations of behaviour over time.
3. Measuring cognitive abilities: Many forms of cooperative behaviour require a high degree of cognitive abilities, such as the ability to communicate, remember social relationships, and anticipate the behaviour of others (Platt, Seyfarth and Cheney, 2016; Melis and Rossano, 2022). Measuring these cognitive abilities in primates therefore requires careful experimental design and interpretation of results.
4. Separating cooperation from other social behaviours: Cooperative behaviour often occurs alongside other social behaviours, such as aggression, competition, and dominance (Flack *et al.*, 2006). Separating the effects of these other behaviours from the effects of cooperation can be difficult, as they may be closely intertwined.

5. Studying natural behaviour in controlled settings: Many studies of primate cooperation are conducted in controlled laboratory and captive settings, which may not accurately reflect the natural behaviour of the primates in the wild (Lopresti-Goodman and Villatoro-Sorto, 2023). Existing primate cooperation research has primarily focused on assessing dyadic cooperation and does not explore group-level cooperation (Williams, Shultz and Jensen, 2022). Accounting for the effects of captivity and experimental conditions can be challenging, and may require researchers to combine or link laboratory experiments with field observations.

Despite the challenges outlined above, researching primate cooperative behaviour has and continues to be important for a number of reasons. 1) research has been used to inform theoretical concepts used to explain human development and complex human societies (Cronin and Sánchez, 2012); 2) exploring cooperative behaviour of primate species can be used to inform captive primate husbandry, maintaining and improving welfare standards (Lopresti-Goodman and Villatoro-Sorto, 2023); 3) understanding the cooperative behaviour of primate species can also be used to inform conservation management programmes with the aim of preserving endangered primates (Marshall and Wich, 2016).

It is important that, through further research, gaps in our existing knowledge are addressed to inform how taxa appropriate cognitive enrichment should be incorporated in standard husbandry practice, with the aim of improving captive welfare (Clark, 2017) and that behavioural research informs and develops conservation strategies (Marzluff and Swift, 2017).

Research investigating the explanatory mechanisms of cooperation distinguishes between direct and indirect benefits of cooperative behaviour whilst acknowledging that they are not necessarily mutually exclusive (Figure 1). An exploration of kin selection, mutualism and reciprocity as mechanisms of cooperation follows.

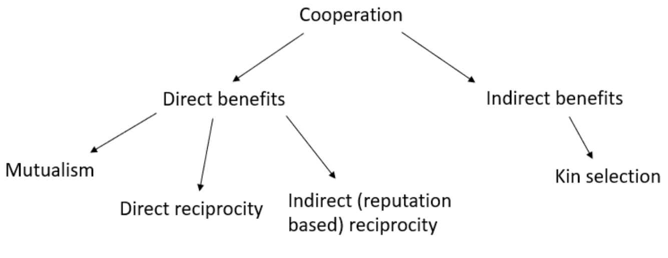

Figure 1: Explanations of cooperation. Direct benefits explain mutually beneficial cooperation, indirect benefits explain altruistic cooperation. Direct and indirect benefits are not necessarily mutually exclusive (modified from West, Griffin and Gardner, 2007).

1.2 Kin selection

Kin selection theory is a concept within evolutionary biology that seeks to explain the occurrence of altruistic and cooperative behaviours in nature (Birch and Okasha, 2015). Developed by Hamilton in the 1960s, kin selection theory provides an explanation for why animals may exhibit self-sacrificing behaviours that benefit their relatives, even at the expense of their own survival or reproduction (Birch and Okasha, 2015). Kin selection theory proposes that individuals have an evolutionary incentive to help others they are genetically related to (Kramer and Meunier, 2016). The theory relies on the concept of inclusive fitness, which takes into account an individual's own reproductive success (direct fitness) and the reproductive success gained through the survival and reproduction of individuals who share a proportion of their genetic material (indirect fitness) (Kramer and Meunier, 2016).

Kin selection as an explanation of cooperation, relies on the assumption that related individuals gain either direct or indirect fitness as a result of cooperative behaviour (Clutton-brock *et al.*, 2002). It is considered that the proportion of relatedness and shared genes can be used to explain and predict cooperation (West *et al.*, 2002). This is based on Hamilton's Law which predicts that individuals favour, support and cooperate with those more closely related to themselves, those with whom they share more genes (Das, 2021), preferential treatment of kin is referred to as nepotism (Chapais, 2001).

Cooperative behaviour is commonly attributed to kin selection (Langergraber *et al.*, 2007) with evidence and examples of nepotistic biases for cooperative behaviour being recorded across primate species (Silk, 2009). Allonursing, observed in wild gray mouse lemurs (*Microcebus murinus)* has been attributed to kinship determining cooperative breeding behaviour (Eberle *et al.*, 2023); Chimpanzees (*Pan troglodytes)* are thought to favour closely related males to form affiliative partnerships for prey hunting and territorial defence (Mitani, Merriwether and Zhang, 2000) and coalition formation in Barbary macaques (*Macaca Sylvanus)* suggests males are more likely to intervene when conflict involves related individuals (Widdig Streich and Tembrock, 2000). Chapais (2001) proposes there is strong evidence that mother-offspring interactions are shaped by kin selection, and notes that reciprocity between kin decreases significantly when coefficients of relatedness are 0.25 and below. Research by Perry *et al.,* (2008) investigating kin-biased social behaviour, including coalition formations of wild adult female *C. capucinus,* reported that maternal relatedness of 0.25 and above was significantly associated with social dyad formations. This research reported that paternal relatedness had weak or no effect on coalition formations and speculated that this is either because *C. capucinus* are unable to recognise paternal kin or that they do not favour paternal kin in reciprocal behaviour (Perry *et al.*, 2008). Interestingly, research by Tombak *et al.,* (2019) suggests that within despotic primate societies, kinship maintains an unequal distribution of cooperative behaviour, which may have negative fitness consequences. Tombak *et al.,* (2019) also propose that in egalitarian primate societies, social behaviour is regulated by reciprocity. Kin selection theory is considered a satisfactory explanation of nepotistic cooperation (Clutton-

Brock, 2009) and is commonly used to explain the cooperative behaviour of chimpanzees and other socially intolerant species where, cooperation between non-kin is rare or non-existent (Tan and Hare, 2017). However Silk (2009, p. 3243) argues that other mechanisms, such as reciprocity and mutualism

> *"…may compliment the effects of kin selection and amplify the extent of nepotistic biases in behaviour."*

In socially tolerant species, the occurrence of non-kin cooperation calls for alternative explanations (Silk, 2009). Historically, primatologists have faced difficulties with estimating and measuring relatedness in wild and captive populations, largely due to unknown information of paternal kinship (Silk, 2006) which may therefore have contributed to the misattribution of kin selection theory. This therefore raises questions around the reliability of kinship alone as an explanation of cooperative behaviour (Silk, 2006) which is supported by the notion that kinship has been over emphasised, overestimated and often unquestioned (Chapais, 2001, 2006). It has been suggested that the overemphasis of kin selection, has seen alternative and or additional contributing explanations of cooperative behaviour being overlooked or ignored and does not explain growing evidence suggesting that complex cooperation is just as likely to occur between non-kin across a range of taxa (Griffin and West, 2002; Langergraber *et al.*, 2007).

1.3 Mutualism

As a theoretical concept, mutualism is considered a relatively simple explanation of cooperative behaviour, based on the idea that individuals involved in cooperative acts, benefit from the outcome (Boesch, Boesch and Vigilant, 2006; van Schaik and Kappeler, 2006). Evidence has been documented across a range of taxa and includes mutualistic acts between both interspecifics and conspecifics (Stachowicz, 2001).

1.3.1 Interspecific mutualism

Interspecific mutualism is considered ubiquitous, with symbiotic interactions occurring between species in all ecosystems (Bshary and Bronstein, 2004; Bascompte, 2019). It is suggested that interspecific mutualism has:

> *"… played a major role in the diversification of life on Earth... but the relationships between mutualism and diversity are not yet clear…"* (Bascompte, 2019, p. 467).

Producing benefits across species, accepted examples include: symbiotic relationships between plants and pollinators (Bascompte, 2019) and shared predator alarm calling between Bluish-slate antshrike (*Thamnomanes schistogynus*) and Saddle-back tamarins (*Leontocebus weddelli*) (Martínez *et al.*, 2022). The symbiotic relationship between frugivore primates and plant and tree seed dispersal is an example of the importance of interspecific mutualism (Gómez and Verdú, 2012; Nevo and Valenta, 2018). Chapman (1995) suggested that continued hunting and depletion of wild primates has significant implications for the future of forest habitats. Thus, illustrating the importance of interspecific mutualism to maintain and protect ecosystems and biodiversity. This is specifically true of *M. nigra* who have a mutualistic ecological role in on the island of Sulawesi (Gómez and Verdú, 2012). However, habitat fragmentation and habitat loss is negatively impacting on the geographical range of this species, which in turn could threaten current and future biodiversity of the island (Gómez and Verdú, 2012).

1.3.2 Dyadic mutualism

Mutualism among conspecifics, commonly occurs within existing, stable dyads, where cooperative acts result in mutual fitness benefits (van Schaik and Kappeler, 2006; Taborsky *et al.*, 2016). In dyadic mutualism, cheating and defection rates are considered relatively low due to the long-term fitness gains and benefits of cooperating (van Schaik and Kappeler, 2006). The cooperative agonistic coalitions of male Assamese macaques (*Macaca assamensis*), provides an example of dyadic mutualism. Cooperatively, males display and direct aggression towards target males, the success and strength of these coalitions have been linked to successful breeding, specifically, the number of offspring sired, this is irrespective of individual dominance ranking (Schülke *et al.*, 2010). The research on *M. assamensis* also demonstrated the absence of a strong kin bias (Schülke *et al.*, 2010). Thus, indicating the importance of social bonding, coalition forming and conspecific mutualism to the individual fitness of male *M. assamensis*.

1.3.3 Group-level mutualism

In social species, group-level mutualism is particularly important, because behaviour can have both short-term and lifetime fitness consequences for the whole group (West, Griffin and Gardner, 2007). Coordinated group actions can provide significant benefits, including for example: cooperative group hunting, group predator defence and shared resource exploitations. Group hunting in Taï chimpanzees (*Pan troglodytes verus*) has been attributed to mutualism, with meat distribution strongly associated with the level of hunting behaviour contributed (Boesch, Boesch and Vigilant, 2006). Conversely, in Gombe chimpanzees (*Pan troglodytes schweinfurthii*), meat distribution is related to social dominance, with higher-ranking individuals gaining greater benefits regardless of their level of contribution to the hunting act (Boesch, Boesch and Vigilant, 2006). Therefore, what is apparent, is the variability of group-level mutualism and associated fitness outcomes.

In contrast to strong dyadic mutualism, group-level mutualism is described as having frequent ‘free riders’, individuals who do not contribute to cooperative acts but still gain a benefit (van Schaik and Kappeler, 2006). This is known as a by-product benefit, and was acknowledged in a study of ring-tailed lemurs (*Lemus catta*), where individuals of the group, despite not engaging in territorial defence behaviour, still benefitted by being able to forage in the defended territory (Nunn and Deaner, 2004). By-product mutualism does not rely on or require stable bonds or relationships (van Schaik and Kappeler, 2006).

1.3.4 Cheating and punishment

There remains a debate around whether cheating behaviour is adaptive within cooperative animal societies (Riehl and Frederickson, 2016). Cheaters benefit from the cooperative behaviours of others without contribution, which is why previous assumptions linked cheating behaviour with increased fitness for cheaters and reduced fitness for co-operators. However, Riehl and Fredrickson (2016) contend that cheating, instead, lowers fitness due to associated punishments which have evolved in response to cheating behaviour. If cheating behaviour was completely adaptive, it is argued that cooperative behaviour would not have evolved and endured so prolifically in animal societies (Clutton-brock *et al.*, 2002). Therefore, the benefits of cooperating weighed against punishments for defecting, maintain cooperative behaviour (Boyd, Gintis and Bowles, 2010). An explanation for the persistence of cheating behaviour is linked to deception, where individuals adopt tactical deception behaviour to avoid conspecific detecting their cheating behaviour (Le Roux *et al.*, 2013). Tactical deception has been reported in chimpanzee studies, investigating cooperative food sharing, and has included evidence of both initial and counter deception tactics (Kirkpatrick, 2007). Comparative studies investigating tactical deception in non-human primates, suggests that varying levels of deception are associated with cognitive ability and has determined the social evolution of primate species (Byrne and Whiten, 1992). In a review of non-human primate cooperative interactions, Riehl and Fredrickson (2016) found that free-riding behaviour was correlated with dominance ranking and kinship, providing alternative explanations for the prevalence of cheating/defecting behaviour. In primate species with strong dominance hierarchies, dominant individuals use their status for priority access to resources irrespective of their contribution in cooperative acts, and free-riding behaviour is accepted by lower ranking individuals (Cummins, 1999). In terms of free-riding and cheating behaviour related to kinship, this demonstrates a level of tolerance between related individuals that could be explained by and linked to indirect fitness.

In conclusion. there are immediate, demonstratable benefits of mutualistic acts, which do not require animals to keep track of owed pay backs (Boesch, Boesch and Vigilant, 2006). However, this simplistic concept of symbiotic relationships, may fail to address or explain more complex levels of interactions and cooperative behaviour.

1.4 Reciprocity

The evolutionary origins of cooperative behaviour have been extensively debated and at the centre of this debate is cooperation between non-kin, a phenomena that undermines previously accepted nepotistic explanations of helping behaviour (Pennisi, 2005). The over-reliance on nepotistic explanations for cooperative behaviour could be due to inference drawn from vast research that predominately focussed on studying helping behaviour in populations with close related individuals (Taborsky *et al.*, 2016). Therefore a bias of evidence for cooperative behaviour between related individuals may exist, neglecting scientific investigation of helping behaviour between non-kin (Taborsky *et al.*, 2016).

Reciprocity is considered an important explanatory mechanism for non-kin cooperation, whereby individuals exchange helping behaviour on the basis of ‘you scratch my back, I’ll scratch yours’ (Trivers, 2006; O’Hearn *et al.*, 2022). There is a long standing argument between two competing viewpoints; that reciprocity is only evident in humans and those who argue that reciprocity is omnipresent in non-human animals (Schweinfurth and Call, 2019a).

Conclusive evidence of underlying mechanisms for reciprocity in non-human animals is difficult to obtain and therefore controlled experimental investigation is needed (Taborsky *et al.*, 2016). However, whilst experimental design allows for conditions to be controlled, questions over ecological validity are raised (Jaeggi and Gurven, 2013a). Reciprocity in non-human animals is commonly documented in a reproductive context (Díaz-Muñoz *et al.*, 2014) however, reciprocity is not restricted to cooperative breeding behaviour alone (Schweinfurth and Call, 2019b). Table 2 presents examples of published literature providing evidence of reciprocal cooperation across a wide range of vertebrates, in both natural and experimental studies. The studies in table 2 investigating primate reciprocity, have predominately focussed on investigating allogrooming behaviour to establish evidence of reciprocity. A discussion addressing the underlying assumptions of generalised, direct and indirect reciprocity follows. Whilst these are addressed separately, they are not necessarily mutually exclusive, which poses challenges to researchers trying to detect and distinguish between multiple forms of reciprocity (Majolo, Schino and Aureli, 2012; O’Hearn *et al.*, 2022).

Table 2: Examples of reciprocal cooperation in vertebrate, including studies performed in the natural field, laboratories or zoos and either under controlled experimental conditions or via observations. This table represents a selection of published studies and is not an exhaustive list (modified from Taborsky (2016)).

Species	**Common name**	**Reciprocal behaviour**	**Form of reciprocity**	**Obs/ Exp**	**Field/ Lab/Zoo**	**Reference**
Tyto alba	Barn owl	Allopreening and food exchange	Direct	E	F	(Roulin *et al.*, 2016)
Phoeniculus purpureus	Green woodhoopoe	Allopreening	Direct	O	F	(Radford and Du Plessis, 2006)
Cantorchilus leucotis	Buff-breasted wren	Allopreening	Direct	O	F	(Gill, 2012)
Desmodus rotundus	Common vampire bat	Reciprocal food sharing	Generalised	E	L	(Carter, 2013)
Apodemus microps	Herb-field mouse	Allogrooming	Direct	O	L	(Stopka and Graciasová, 2001)
Rattus norvegicus	Norway rat	Reciprocal food exchange	Direct	E	L	(Dolivo and Taborsky, 2015)
Tursiops aduncus	Indo-Pacific bottlenose dolphin	Reciprocal flipper rubbing	Generalised	O	F	(Sakai *et al.*, 2006)
Aepyceros melampus	Impala	Allogrooming	Direct	O	F	(Mooring and Hart, 1997)
Eulemur fulvus	Red-fronted lemur	Allogrooming	Direct	O	F	(Port, Clough and Kappeler, 2009)
Saguinus oedipus	Cotton-top tamarin	Food exchange, allogrooming	Indirect	E/O	L	(Hauser *et al.*, 2003)
Cebus capucinus	White-faced capuchin	Allogrooming	Direct	O	F	(Manson *et al.*, 2004)
Macaca fascicularis	Long-tailed macaque	Allogrooming	Direct	E/O	L	(Majolo, Schino and Aureli, 2012)

Table 2 (continued)

Species	**Common name**	**Reciprocal behaviour**	**Form of reciprocity**	**Obs/ Exp**	**Field/ Lab/Zoo**	**Reference**
Macaca Sylvanus	Barbary macaques	Allogrooming	Direct	O	F	(Carne, Wiper and Semple, 2011)
Macaca fuscata	Japanese macaque	Allogrooming	Attitudinal	O	L	(Schino, Di Sorrentino and Tiddi, 2007)
Macaca nigra	Sulawesi black crested macaque	Allogrooming	Direct	O	Z	(Dunayer *et al.*, 2019)
Macaca thibetana	Tibetan macaque	Allogrooming	Direct	O	F	(Balasubramaniam *et al.*, 2011)
Pongo pygmaeus	Orangutan	Reciprocal token exchange	Calculated	E	L	(Dufour *et al.*, 2009)
Pan troglodytes	Chimpanzee	Reciprocal food exchange, allogrooming	Direct Attitudinal	O/E	L/F	(Hemelrijk and Anneke, 1991) (Gomes, Mundry and Boesch, 2009) (Engelmann, Herrmann and Tomasello, 2015)

1.4.1 Generalised reciprocity

When helping behaviour becomes the norm in a population, this is said to be indicative of generalised reciprocity. Due to cooperation being essential, helping behaviour is common place and individuals recognise the value of and are therefore inclined to help others in order for the population to function effectively (Salazar *et al.*, 2022).

An accepted rule of generalised reciprocity is taken from Taborsky *et al.,* (2016, p. 3):

> *"help anyone if helped by someone"*

Implying, that helping behaviour does not necessarily include a direct repayment for the original helping behaviour. Taborsky *et al.,*(2016) propose that based on an individual's social experience, generalised reciprocity can create stable, consistent and reciprocal cooperative behaviour in social groups. Examples of generalised reciprocity include shared vigilance behaviour, cooperative hunting and food sharing, whereby, collective helping behaviour is an effective, adaptive strategy. It is predicted that generalised reciprocity is more common in egalitarian societies, research comparing reciprocal food sharing in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), concluded that despotic dominance in bonobos, reduced the frequency of reciprocal behaviour (Jaeggi, Stevens and Van Schaik, 2010).

Empirical studies of generalised reciprocity in primates have produced varied results and comparative research is challenging due to multiple factors including, different experimental conditions and previous social interaction experience of participants. Research investigating the connection between allogrooming and coalitionary support was carried out with a group of 81 unrelated female rhesus macaques (*Macaca mulatta)* at Cayo Santiago research field station (O'Hearn *et al.*, 2022). The study investigated the response of individuals to simulated calls for coalitionary support in exchange for grooming. The study concluded there was no evidence of generalised reciprocity, however, it is worth noting that O'Hearn *et al.,* (2022, p. 9) concluded that:

> *"the absence of evidence is not evidence of absence"*

The researchers acknowledged limitations of their study, for example a small sample size limiting the ability to detect weak response signals (O'Hearn *et al.*, 2022). It is also proposed that the perceived high costs/risks associated with coalition behaviour, far outweigh any benefits associated with allogrooming behaviour and could therefore explain the lack of reciprocity. Specifically, in despotic species such as *M. mulatta*, increased risks of injury may be a determining factor in rates of observed generalised reciprocity, where benefits are outweighed by the costs (O'Hearn *et al.*, 2022). This theory was corroborated by Schino *et al.* (2007) who also reported that grooming did not promote coalitionary support in another despotic species, Japanese macaques (*Macaca fuscata*). With differing levels of social tolerance identified across primate species, it is likely that this will be a contributing factor to the presence of generalised reciprocity (De Waal and Suchak, 2010).

Leimgruber *et al.,* (2014, p. 5) examined and compared 'pay it forward behaviour' using an identical novel apparatus for a group of children under the age of four and a group of four capuchin monkeys (*Cebus apella*) who were part of the Yale Comparative Cognition Laboratory colony. Participants were allocated roles; an Actor was able to manipulate the apparatus and determined the allocation of rewards between the Actor and Recipient (the second participant who could not manipulate the apparatus and received an allocation determined by the Actor). Leimgruber *et al.,* (2014) concluded that there was evidence of generalised reciprocity associated with a "*give-what-you-get-mechanism"*. The study suggested that the act of paying it forward behaviour, observed in both the children and capuchin subjects, is established on a contingency-based form of generalised reciprocity. This mechanism is considered cognitively simple, not requiring complex social cognition, for example, perspective taking abilities and computing of outcomes (Leimgruber *et al.*, 2014; Schweinfurth and Call, 2019b). Due to being less cognitively complex, generalised reciprocity is considered an explanation for group-level cooperation and provides a foundation for more complex cooperative behaviours to develop (Leimgruber *et al.*, 2014).

Jaeggi and Gurven (2013b) concluded that reciprocity was a significant determining factor for helping behaviour in both humans and non-human primates. The study compared food and commodity sharing behaviour, and argues against using cognitive constraints to explain differences in reciprocal behaviour in primates because they propose that not all reciprocal behaviour is cognitively demanding nor requires score keeping memory ability. Instead they suggest that differences relate to the species specific fitness benefits of reciprocity correlated with kinship and rank. This research did not test for generalised reciprocity and only compared acts of direct reciprocity (Jaeggi and Gurven, 2013c).

1.4.2 Direct reciprocity

Direct reciprocity is a social interaction where one individual will help another, with the expectation that they will receive help in return (Majolo, Schino and Aureli, 2012). Direct reciprocity is widely seen in humans and non-human animals and employs a tit-for-tat strategy, based on the idea that cooperation is beneficial for both parties involved (Taborsky *et al.*, 2016). Direct reciprocity is considered a stable mechanism of cooperation, as it is built on mutual trust that helping behaviour will be reciprocated. The underlying rule in direct reciprocity is to help someone who has previously helped you (Taborsky *et al.*, 2016).

A meta-analysis of allogrooming in 14 primate species across 25 different social groups, reported that direct reciprocity played a more important role than kinship in determining allogrooming behaviour (Schino and Aureli, 2010b). The study emphasised reciprocity as the determining factor for primate social interactions and further highlighted that evidence exists of reciprocal partner choice, whereby individuals maximise benefits by direct reciprocation. The researchers did not investigate the role of generalised reciprocity, which could be a factor across the studies (Schino and Aureli, 2010b). All of the studies analysed were based on captive primate groups, some of which had relatively small group sizes, the smallest being a group of four ring-tailed lemurs (*Lemur catta*), both factors therefore raise some questions around the ecological validity of the findings. Another meta-analysis of 22 primate species across 48 social groups concluded that female primates are more likely to groom individuals that they have been groomed by, supporting the concept of direct reciprocity as a mechanism for cooperation (Schino and Aureli, 2008). As the research only included female subjects, the study could only compare the significance of reciprocity against maternal kinship. Schino and Aureli (2008) suggest that whilst their findings provide strong evidence in favour of direct reciprocity over kinship, this creates a challenge for behaviourists to establish how individuals choose partners to cooperate with. Research by Dunayer *et al.,* (2019) on a group of eight captive female black crested macaques (*Macaca nigra)* concluded that, direct reciprocity could be used to explain grooming behaviour within the group. This study investigated the effects of delays between helping behaviour and concluded that long-term delays impeded the ability to easily distinguish mechanisms of reciprocity (Dunayer *et al.*, 2019).

1.4.3 Indirect reciprocity

Indirect reciprocity is an example of group-based cooperation and is a key mechanism used to explain helping behaviour between non-kin (Santos, Pacheco and Santos, 2021). Indirect reciprocity is a process in which individuals benefit from helping others, even if the individuals have never interacted before and will never interact directly again. This form of reciprocity occurs when third parties vicariously observe interactions between other individuals and are then willing to help the original helper, this requires complex processing of social information (Santos, Pacheco and Santos, 2021). Indirect reciprocity does not require the same strict conditions of social interactions as those applied in kin selection and direct reciprocity (Okada, 2020). The underlying rule of indirect reciprocity is help someone who is helpful (Taborsky *et al.*, 2016).

Indirect reciprocity is considered necessary to maintain stable social environments and is therefore an adaptive phenomenon, which increases overall survival and genetic success. It is beneficial for individuals living in social groups to build, maintain and improve their reputation by cooperating (Roberts, 2008; Taborsky *et al.*, 2016), this form of reciprocity encourages prosocial cooperative behaviour. Indirect reciprocity has been used as a mechanism to explain complex cooperative behaviour in humans with research investigating determining factors such as: reputation spread; interaction observability and empathy (Taborsky *et al.*, 2016). Because of the complexities surrounding indirect reciprocity it poses several challenges for behavioural research and therefore theorical models have predominately focused on and been applied to human behaviour only. In fact, Schino *et al.,* (2021, p. 1) suggested

> *"…animal research has produced little or equivocal evidence of indirect reciprocity."*

Primates are considered suitable for investigating indirect reciprocity due to their social grouping and complex social behaviour. Evidence of limited indirect reciprocity in primates was reported by Majolo *et al.,*(2012)*,* their research concluded that direct reciprocity was the predominant mechanism explaining exchanges of grooming behaviour of long-tailed macaques (*Macaca fascicularis*). Whilst they provided strong evidence of direct reciprocity, they also reported some albeit limited evidence of indirect reciprocity. Majolo*,* Schino and Aureli,(2012) established that individuals received more bouts of grooming from bystanders after giving grooming. The researchers did acknowledge however, that their results might have been affected by time constraints associated with the experimental design and spatial proximity of the captive primates (Majolo, Schino and Aureli, 2012). Figure 2 summarises the theoretical process of indirect reciprocity, illustrating observers and bystander positions in a social network. It follows that capturing evidence of complex social interactions and associated outcomes, provides a real challenge to researchers.

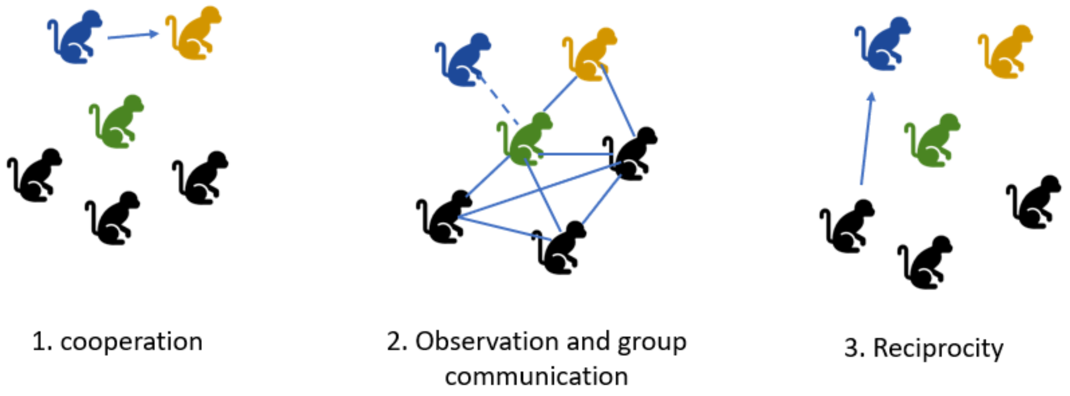

Figure 2: Indirect reciprocity can stabilise cooperative behaviour. (1) an individual (blue primate) cooperates with another (yellow primate). (2) Within a population, observers (e.g. green primate) vicariously observes behaviour, processing social information and taking into account the reputation of the yellow primate. The green primate shares that information with other group members/bystanders (black primates). (3) Information about the blue primates previous behaviour may influence the behaviour of others towards blue primate in the future (modified from Santos, Pacheco and Santos, 2021).

Comparative research by Schino *et al.,* (2021) concluded that tufted capuchin monkeys (*Cebus apella*) did not engage in indirect reciprocity for either grooming or food sharing behaviour. Instead they attributed grooming behaviour to social facilitation and observed that receipt of grooming increased after giving grooming (Schino *et al.*, 2021). Similarly, a study of wild Barbary macaques (*Macaca Sylvanus*) reported that grooming exchanges were associated with direct reciprocity and found no evidence of generalised or indirect reciprocity (Molesti and Majolo, 2017).

It is suggested that the cognitive constraints of animals may impede the understanding and ability to spread complex social information associated with engaging in indirect reciprocity (Schino *et al.*, 2021). However, in a study investigating common marmoset (*Callithrix jacchus*) sensitivity to third party reciprocity, the researchers reported that the marmosets accepted rewards less frequently from non-reciprocators and in fact favoured rewards from observed reciprocators (Kawai *et al.*, 2014). This supports, in part, the theoretical model of indirect reciprocity illustrated in Figure 2. The research suggested that the ability to detect unfairness was not associated with cognitive abilities of this species and explained it instead, from a pro-social perspective (Kawai *et al.*, 2014). Schino *et al*., (2021) argue that evidence of indirect reciprocity in non-human animals is inconclusive and furthermore, proposed that the little evidence that does exist is only observed in animals that live in small, cohesive societies, which enables individuals to monitor and observe the behaviour of others.

Despite finding limited evidence of indirect reciprocity, Majolo, Schino and Aureli (2012) contend that the mechanisms of reciprocity are not mutually exclusive and that all three types of reciprocity are theoretically plausible. Furthermore, Berra (2014) maintains that it is erroneous to assume that reciprocity can be explained and limited by the strategic capabilities of species and propose further exploration of the contagion of reciprocity be explored.

1.4.4 Attitudinal reciprocity

Research studying food sharing behaviour in brown capuchins (*Cebus apella*) reported that females are more likely to engage in reciprocal behaviour than males and proposed a hypothetical explanatory mechanism named 'attitudinal reciprocity' (de Waal, 2000). Attitudinal reciprocity is associated with social predispositions, where individuals mirror behavioural responses of others, for example, if individual A reacts positively towards B, B will act positively towards A (de Waal, 2000). Also known as emotionally based reciprocity, attitudinal reciprocity is determined by social bonding (Schino and Aureli, 2010a) and was supported by Hattori and Kuroshima (2005) who used the concept to explain why individuals would accept temporary unequal rewards, providing equity was established later.

1.4.5 Concluding comments

It is proposed that reciprocity is a diverse phenomenon, the mechanisms and strategies of which differ and are not mutually exclusive. It is acknowledged that complex psychological mechanisms are necessary to initiate and maintain reciprocal behaviour, including for example numerical quantification, delayed gratification and the ability to detect cheaters (Stevens and Hauser, 2004). Stevens and Hauser (2004) suggest that cognitive limitations constrain reciprocal behaviour in non-human animals. The notion that reciprocity is too cognitively challenging for non-human primates appears to be based on research that has predominately tried to separate and differentiate mechanisms (Schweinfurth and Call, 2019b).

Revisiting O'Hearn *et al.,* (2022) and their statement that a lack of evidence does not necessarily mean the absence of reciprocity, there is a need for continued research to improve our understanding of reciprocal behaviour in non-human primates. Investigating mechanisms of reciprocity in non-human animals is very challenging, and experimental designs create contingent factors that may affect results.

The lack of existing evidence of indirect reciprocity in non-human primates could be explained by a number of factors other than it simply does not exist (1) research has predominately focused on distinguishing and elevating human behaviour and intelligence (2) an historical viewpoint linked to non-human primate cognitive capabilities (3) confounding variables faced when investigating reciprocity in non-human animals.

1.5 Primate cooperation experiments

Research investigating primate cooperation has predominately used controlled experimental conditions to find evidence of, and to explore explanatory mechanisms of cooperative behaviour in non-human primates (Albiach-Serrano, 2015). The purpose of much of this research, has been to inform and develop models for investigating and explaining human cooperation (Albiach-Serrano, 2015).

A popular experimental method used to investigate cooperative behaviour of primates is the cooperative pulling paradigm, which assesses the ability of two or more individuals to work together in a pulling task to access food rewards (Williams, Shultz and Jensen, 2022). Cooperative rope-pulling experiments have been a widely accepted methodology used in comparative psychology since they were first introduced by Crawford in 1937, who investigated the ability of chimpanzee subjects to simultaneously pull ropes attached to a weighted box, baited with food (Albiach-Serrano, 2015). Crawford's initial research suggested that the subjects were unable to spontaneously synchronise rope-pulls and therefore, subsequent training phases were introduced (Albiach-Serrano, 2015). Table 3 indicates that research of non-human primate cooperation, continues to favour the use of rope-pulling tasks and studies predominately include training phases as part of the experimental design (Albiach-Serrano, 2015). Species physiology and captive environment are aspects for consideration when developing cooperative pulling tasks, as such there is variation in the apparatus used (Figure 3). This variation could account for some of questions raised about the reliability of the cooperative pulling paradigm as a comparative tool (Jacobs and Osvath, 2015).

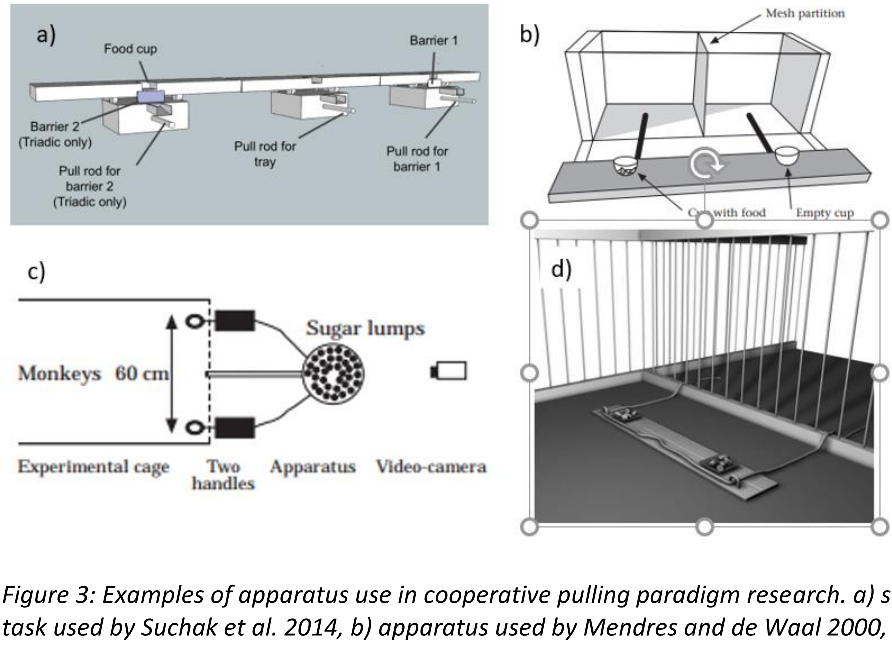

Figure 3: Examples of apparatus use in cooperative pulling paradigm research. a) simultaneous pulling task used by Suchak et al. 2014, b) apparatus used by Mendres and de Waal 2000, c) rope-pulling task used by Chalmeau et al., (1997) and d) cooperation apparatus used by Melis, Hare and Tomasello, (2006).

There are a number of factors that affect individual performance in a rope-pulling task, those relating to this study are discussed. Firstly, age, Jacobs and Osvath (2015) suggest that older, more cognitively developed animals often perform better in cooperative rope-pulling tasks, however, success has also been related to persistency in juvenile subjects. A cooperative pulling study of *C. apella* by de Waal and Davis (2003) did not report age as a determining factor for successful cooperation and instead emphasised the importance of dominance rank and kinship. Partner choice is another factor, and like the de Waal and Davis study, most of the research using cooperative pulling tasks outlined in Table 3, controlled the pairings of subjects. Whilst these studies do not indicate that controlled dyadic pairings of individuals negatively affected cooperation success, by including prior training, the researchers are unable to establish whether individuals have the innate cognitive skills necessary to cooperate or if partner choice has an effect on the success rate of cooperation. Research by Suchak *et al.,* (2014, p. 1) investigated chimpanzee free partner choice in a pulling task and concluded that subjects:

> *"…preferentially approached the apparatus when kin or nonkin of similar rank were present, showing a preference for socially tolerant partners."*

This research provides evidence that the chimpanzee subjects made choices of who they would cooperate with, this is further supported by Martin *et al.,* (2021) who reported that partner choice was positively associated with success of common marmosets (*Callithrix jacchus*) in a cooperative pulling task. Research by Mendres and de Waal (2000) suggests that the presence of a partner is important and reported that the rope-pulling rates of *C. apella* increased in the presence of others, this supports the concept of presence-dependent cooperation and will be investigated in this study. Comparative research has also suggested that social tolerance, including social structures and social behaviours, is a key determining factor of cooperation (Petit, 1992; Schmelz and Call, 2016; Martin *et al.*, 2021). Variability of cooperative behaviour across and within primate species, has been attributed to individual social tolerance levels (Martin *et al.*, 2021).

The studies outlined in table 3 have predominately been conducted in primate research facilities using subjects that are familiarised with cognitive research experiments and who have had prior training as part of the experimental design. The controlled environment, artificial nature and extensive use of training in pulling paradigm experimental design and methodologies, raises questions relating to the ecological validity of these cooperation studies (Marshall-Pescini *et al.*, 2016). This study will adapt existing accepted methodologies, whilst attempting to mitigate factors affecting ecological validity by, allowing all subjects free partner choice, allowing choice to engage with the cooperative device, presenting the device in the subjects usual housing environment and excluding any training.

Table 3: Examples of cooperation research in primate species, reported in peer-reviewed literature. Created from literature review using Web of Science, Primo and Google Scholar, using the search terms: experimental primate cooperation.

Species	**Common Name**	**No. of subjects**	**Dyad/ Grouping**	**Related or unrelated**	**Captive born**	**Cooperative Task**	**Partner Choice**	**Successful cooperation**	**Attributed to social tolerance**	**Attributed to kinship**	**Training used**	**Reference**
Cebus apella	Tufted capuchin	5	Adults M & F	Mixed	Unknown	Pulling	Yes	Yes	Yes	No	Yes	(Chalmeau *et al.* 1997)
Cebus apella	Tufted capuchin	24	Adults & Juveniles M & F	Unknown	Unknown	Food sharing	No	Yes	Yes	Not analysed	No	(de Waal 1997)
Cebus apella	Tufted capuchin	14	Adults & Juveniles M & F	Mixed	Unknown	Pulling	No	Yes	Yes	No	Yes	(Mendres and de Waal 2000)
Cebus apella	Tufted capuchin	16	Adults & Juveniles M & F	Mixed	Unknown	Pulling	No	Yes	Yes	No	Yes	(Mendres and de Waal 2000)
Callithrix jacchus	Common marmoset	8	Adults M & F	Related	Yes	Pulling	No	Yes	Yes	No	Yes	(Werdenich and Huber 2002)
Pan troglodytes	Chimpanzee	12	Adults & Juveniles M & F	Related	Unknown	Pulling	No	Yes	Yes	No	No	(Melis et al. 2006)
Macaca mulatta	Rhesus macaque	5	Adult males	Unknown	Unknown	Joystick	No	Yes	No	No	Yes	(Visco-Comandini et al. 2015)
Cebus apella	Tufted capuchin	14	Adults & Juveniles M & F	Mixed	Unknown	Pulling	No	Yes	Yes	Yes	Yes	(de Waal and Davis 2003)
Macaca fasicularis	Long-tailed macaque	20	Adults M & F	Unknown	Unknown	Pulling	No	Yes	No	No	Yes	(Massen et al. 2010)

Table 3 (continued)

Species	**Common Name**	**No. of subjects**	**Dyad/ Grouping**	**Related or unrelated**	**Captive born**	**Cooperative Task**	**Partner Choice**	**Successful cooperation**	**Attributed to social tolerance**	**Attributed to kinship**	**Training used**	**Reference**
Cebus apella	Tufted Capuchin	6	Adults & Juveniles M & F	Unknown	Yes	Sequence actions	No	Yes	Yes	No	Yes	(Hattori et al. 2005)
Pan troglodytes	Chimpanzee	39	Adults & Juveniles M & F	Unrelated	Unknown	Pulling	No	Yes	Yes	No	No	(Melis et al. 2006)
Pan troglodytes	Chimpanzee	13	Adult Females	Unknown	Unknown	Pulling	No	No	n/a	n/a	Yes	(Brosnan et al. 2009)
Pongo abelii	Orangutan	6	Adults & Juveniles M & F	Related	Yes	Social tool use	No	Yes	No	No	No	(Volter et al. 2015)
Sanguinus oedipus	Cotton top Tamarin	8	Adults M & F	Unrelated	Unknown	Pulling	No	Yes	Yes	No	Yes	(Cronin et al. 2005)
Pan troglodytes	Chimpanzee	12	Adults M & F	Mixed	Unknown	Pulling	No	Yes	Yes	No	Yes	(Sanchez-Amaro et al. 2016)
Pan troglodytes	Chimpanzee	12	Adults M & F	Mixed	Unknown	Pulling	No	Yes	No	No	Yes	(Greenberg et al. 2010)
Sanguinus oedipus	Cotton top Tamarin	8	Adults M & F	Unrelated	Unknown	Pulling	No	Yes	No	No	Yes	(Cronin and Snowdon 2008)
Cebus apella	Tufted Capuchin	16	Adults & Juveniles M & F	Mixed	Unknown	Pulling	No	Yes	Yes	Yes	Yes	(de Waal and Davis 2003)
Pan troglodytes	Chimpanzee	11	Adult 1 M & 10 F	Unknown	Unknown	Pulling	Yes	Yes	Yes	Yes	No	(Suchak *et al.*, 2014)

1.6 Zoos as research facilities

As well as sources of public entertainment and education, for decades, zoos have been used as research facilities, advancing scientific knowledge of genetics, anatomy, physiology and behaviour of animals that would otherwise be impossible to study (Miranda *et al.*, 2023). It is proposed that the knowledge gained from zoo research can be used to (i) improve welfare of captive animals (ii) inform and share best husbandry practice and (iii) inform effective conservation management. Zoos, are therefore considered invaluable research facilities and conservation institutions. Miranda *et al.,* (2023) however, suggest that time constraints, financial budgets and the lack of qualified research staff are all factors associated with the lack of published scientific literature produced by zoos. Thus, for research to increase, investment in conservation research is needed. Interestingly, Miranda *et al.,* (2023) identified that zoos with clear research mission statements, were more productive in scientific research.

Literature suggests, that zoo research is taxonomically biased in favour of mammals despite zoos housing more non-mammal species (Miranda *et al.*, 2023), however, Rose *et al.,* (2019) suggest that the research output of zoos is beginning to diversify. Another interesting aspect is the proportion of zoo research that focuses on species listed within threatened classifications on the IUCN Red List. Research by Escribano *et al.,* (2021, p. 1899) investigating the global trends in research output of zoos and aquariums, reported that out of 13,569 published zoo research articles, 50% concentrated on species with threat levels above near threatened. However, they also acknowledged that species in 'least concern' and 'vulnerable' categories were those most represented in published zoo research. Other issues influencing subject or species selection for zoo-based research is the available sample size and social grouping, these are determining aspects which are considered when addressing the ecological validity of zoo-based research. This indicates that several factors may be influencing species used in zoo research, and that these decisions may not necessarily advance conservation education and management. Historically, zoo research has focused on less-threatened, charismatic species, those commonly found in captive collections and predominately assesses the welfare needs and associated husbandry practice of captive animals, with the aim of sharing results within the zoo community (Escribano *et al.*, 2021). This study looks to investigate welfare and husbandry practice of two species which are important in terms of their conservation status, *M. nigra* are classified as critically endangered and *C. capucinus* are classified as vulnerable (further information provided in sections 1.10 and 1.11).

An area of zoo research that is currently beginning to gain momentum, is animal cognition, this, according to Garcia-Pelegrin, Clark and Miller (2022) has been overlooked in zoo settings. It is believed that zoos are uniquely positioned to facilitate animal cognition research, helping to close the gap between laboratory experiments and wild observational studies. However, it is suggested that current methods of animal cognition research in zoos, remains heavily reliant on laboratory-based methodologies, often requiring high levels of animal training and habitation and in many instances, includes the use of technological devices e.g. computer touchscreens (Egelkamp and Ross, 2019). The use of technological devices in animal behaviour research remains controversial, largely due to the negative perception of animals interacting with unnatural objects and concerns surrounding anthropomorphism and welfare (Garcia-Pelegrin, Clark and Miller, 2022). Research by Whitehouse *et al.,* (2013) investigated the impact of cognitive research on the welfare of a captive group of *M. nigra* housed at Marwell Zoo, and reported that aggressive interactions decreased and lipsmacking (sociopositive behaviour) increased as a result of cognitive testing. The study concluded that cognitive testing did not have any negative welfare impact (Whitehouse *et al.*, 2013). As a field of research, animal cognition has important implications for the welfare of zoo animals and can be used for example to inform species specific, cognitively appropriate enrichment. In addition to a captive welfare tool, Garcia-Pelegrin, Clark and Miller, (2022, p. 3) state that:

> *"The link between cognition and conservation is also a growing field".*

Based on the probability that captive populations will increasingly be relied on, not only to preserve species, but also for reintroduction programmes, zoos need to ensure that animal cognition becomes the focus of zoo research (Garcia-Pelegrin, Clark and Miller, 2022). It is essential that conservation-relevant cognitive abilities of threatened species are studied. These include for example: problem-solving skills, responses to novelty, social cognition and cognitive mechanisms associated with cooperation, all of which are deemed vital for survival in the wild (West, Griffin and Gardner, 2007; Suchak *et al.*, 2016; Rowell, Pillay and Rymer, 2021). Animal cognition research is therefore necessary, to identify and prevent cognitive abilities being lost via the transgenerational effect of captivity (Courtney Jones, Munn and Byrne, 2017).

Whilst the ambition is for zoos to continue to develop as effective conservation research facilities, consideration needs to be given to the potential challenges encountered with zoo research outlined in table 4. Moving forward, zoos need to review their research mission statements to ensure that goals are not only achievable and measurable, but also interrelate to their conservation mission statements.

Table 4: Potential challenges of zoo research (modified from Garcia-Pelegrin, Clark and Miller, (2022)).

Challenge	**Impact on outcome**	**Possible solutions**
Small group size	Reliability of results Reduced statistical power and limited inference	Review experimental design Work with multiple zoos to increase sample size
Predetermined/ controlled social group	Impacts/restricts behaviour Influences social bonding/pairing Restricted social interactions	Work with multiple zoos to increase sample size
Zoo effect (differences between multiple zoos)	Confounding factors such as housing conditions, prior history, climate	Use repeated measures design Use individual animals as own control
Zoo visitors	Interference with research Perception of research	Researcher to remain professional at all times and be prepared to engage positively with visitors Use signage and social media to inform visitors
Husbandry practice	Interference with research	Obtain husbandry schedule Control where possible confounding variables
Enclosure design	Impedes research design/methods Impacts/restricts behaviour	Use to inform experimental design
Habituation to novel objects	Time constraints may not allow for habitation	Design experiment with minimal training requirement
Training	Impacts behavioural responses	Design experiment with minimal training requirement

1.7 Welfare in captivity

Animal welfare in captivity is a critical issue that has gained significant attention in recent years (Mellor, Hunt and Gusset, 2015). As modern conservation organisations, zoos have a responsibility to improve, achieve and maintain high welfare standards of the animals in their care at all times. However, global implementation of animal welfare standards remains challenging, due to cultural influences, varying attitudes and different legislative frameworks in place around the world (Mellor, Hunt and Gusset, 2015; Veasey, 2022).

The five domains model, used by zoos to assess the welfare of animals, was first introduced in 1994 (Mellor and Reid, 1994). The model has subsequently gone through a succession of updates to include and reflect developments in animal welfare science (Mellor and Beausoleil, 2015). The functional domains of the model consider nutrition, physical environment, health and behavioural interactions of animals (Figure 4). It is proposed that captive environments restrict choice, novelty, exploration and sociality which are within behavioural interaction domain of the model. Assessing the welfare impact of these interactions or the lack of these interactions, can be used to inform species specific husbandry practice and conservation management (Mellor *et al.*, 2020).

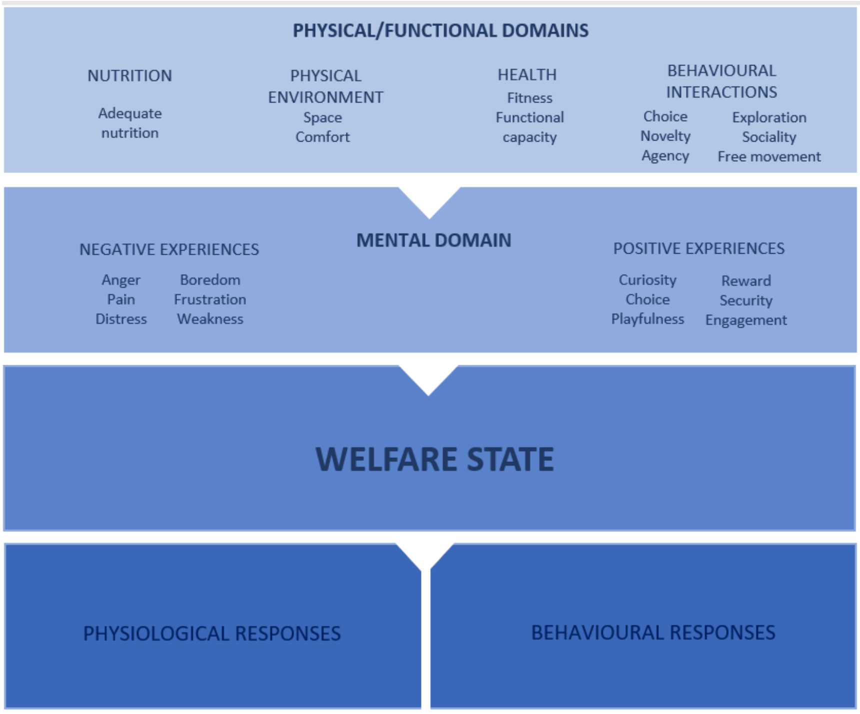

Figure 4: The Five Domains Model, used to assess and monitor animal welfare (modified from Mellor et al., 2020 to include behavioural interactions relevant to this study).

While zoos use both behavioural and physiological responses to assess welfare, the absence of negative indicators of welfare does not necessarily signify positive welfare (Yeates and Main, 2008). For example, the absence of stereotypical behaviour does not indicate positive social affiliation. Thus, animal welfare improvements should not simply focus on identifying negative welfare, but should focus on identifying where opportunities for positive welfare are deprived (Rault *et al.*, 2020). This study will investigate captive *M. nigra* and *C. capucinus* exploration, choice and social behavioural interactions in response to a novel cooperative enrichment device and will assess whether cooperative enrichment is suitable for these species in captivity. Miller *et al.,* (2021) *s*uggest that the inability to express and engage in certain behaviours can compromise welfare and lead to the development of stereotypical behaviour, supporting the need for continued behavioural research in captive settings to inform husbandry practice.

The aspirations of the World Zoo and Aquarium Animal Welfare Strategy are illustrated in figure 5, demonstrating the foundation requirements for survival, including nutrition, appropriate living conditions and safety. Upon these foundations, more varied, complex welfare needs can be addressed and met. The World Zoo and Aquarium Animal Welfare Strategy use the birds taking flight (Figure 5) as a representation of zoos and aquariums retaining and encouraging natural abilities, for many species this includes cooperative behaviour (Mellor, Hunt and Gusset, 2015). Historically, in response to their captive environment, animals have had to adapt their behaviour to enable them to cope, this can result in negative behavioural responses which can include self-directed aggression and other stereotypcial behaviour, which can compromise welfare (Mason, 2010). Providing captive environments that facilitate natural behaviour including choice, mental stimulation and meeting the social needs of captive animals is therefore paramount to positive welfare.

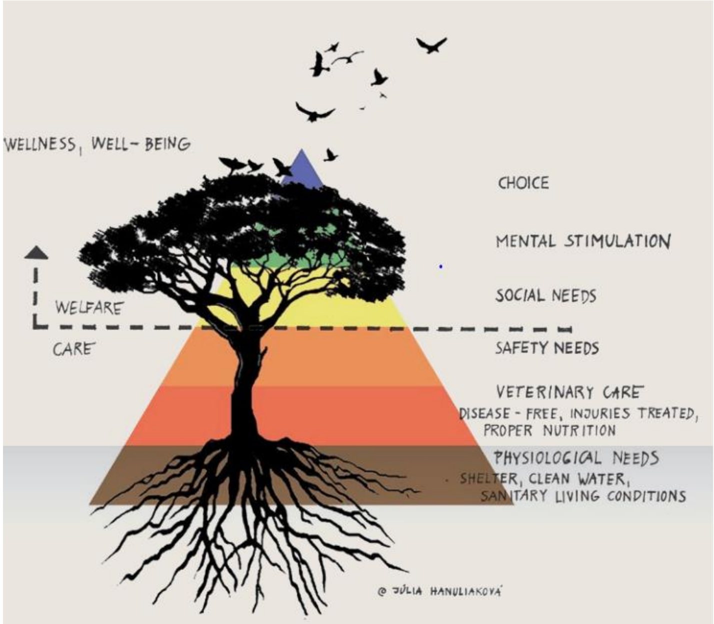

Figure 5: Aspirations of The World Zoo and Aquarium Animal Welfare Strategy, incorporated with Maslow's hierarchy of needs pyramid (Mellor, Hunt and Gusset, 2015).

Whilst requesting members strive to achieve high welfare standards, WAZA also calls on zoos to become welfare leaders, advocates, and advisors, ensuring that positive animal welfare continues to evolve and that developments in animal welfare science are shared within the zoo community (Mellor, Hunt and Gusset, 2015).

1.8 Managing primates in captivity

The IUCN's Species Survival Commission, Primate Species Specialist Group, currently recognise 522 extant primate species (ICUN/SSC Primate Specialist Group, 2021). It is estimated that 65% of these primate species are classified as critically endangered, endangered or vulnerable, making primates one of the most threatened mammalian groups (Fernández *et al.*, 2022). The decline of primates in the wild is primarily due to habitat loss and fragmentation associated with agriculture and hunting (Fernández *et al.*, 2022). This data provides evidence of the need for ex-situ as well as in-situ conservation efforts to protect primate species from extinction. The European Association of Zoos and Aquaria (EAZA) currently manage captive breeding programmes for 81 primate species (Baker and Farmer, 2023).

The effect of the zoo environment, has and continues to receive great interest, and is a growing area of research, however, whilst primate species are considered well represented in zoo research literature, many primates species have been overlooked, with research predominately focusing on great apes (Rose *et al.*, 2019).

Keeping primates in captivity poses several challenges, one of the debates centres around how much captivity should and needs to replicate the natural environment, in order to meet the welfare needs of captive individuals (Hosey, 2005). Captivity can cause abnormal behaviours not recorded in nature, examples include, but are not limited to: regurgitation and re-ingestion in gorillas, body rocking in chimpanzees (Hosey, 2005) and auto-aggression in stump-tailed macaques (*Macaca arctoides*) (Goosen and Ribbens, 1980). Social grouping and husbandry practice are important considerations for managing the welfare of primates in captivity.

1.8.1 Social grouping

In the wild, many primate species live in large, complex social groups (Lopresti-Goodman and Villatoro-Sorto, 2023). In captivity, group size is largely determined and constrained by environmental conditions including for example limited space and housing management considerations (Lopresti-Goodman and Villatoro-Sorto, 2023). Therefore, captive group sizes often differ significantly from social groupings observed in the wild and can have behavioural and welfare implications (Price and Stoinski, 2007). Specifically, Pomerantz, Meiri and Terkel (2013, p. 85) suggest that:

> *… "large-group and wide-ranging primate species are more prone to suffer in captivity".*

Housing primate species in inappropriate small social groups is associated with stereotypical behaviours and is linked with the frustration motivation hypothesis (Pomerantz, Meiri and Terkel, 2013). Restricted sociality, created in captive settings, can result in animals being unable to regulate and express socially related motivations and desires. Pomerantz, Meiri and Terkel (2013) studied 24 species of zoo-housed primates and concluded that, species that naturally live in large groups are more likely to develop stereotypical hair pulling behaviour due to frustration of low availability for social grooming with conspecifics in captive settings. Small groups also restrict complex social networking and can influence the quality of social bonding in a group, social deprivation is linked to causing stress in captive primates (Wolfensohn and Honess, 2005; Hare and Yamamoto, 2015). Behavioural and welfare problems associated with inappropriate group size in captivity, include, but are not restricted to: increased aggression and competition, loss of cooperative behaviour, reproductive issues, sociality issues and stereotypy behaviour (Mallapur, 2005; Price and Stoinski, 2007).

Research recommending optimal group sizes, exists for some primate species. Neal Webb, Hau and Schapiro (2019) investigated the effects of group size and composition, on the behaviour of captive chimpanzees, their findings suggest that groups consisting of seven or more, showed higher levels of locomotion and affiliative behaviour. This research recommended that captive chimpanzees should be housed in large, age-diverse groups with a higher proportion of males (Neal Webb, Hau and Schapiro, 2019). However it is worth noting, this research acknowledged that whilst larger group size provided welfare benefits, smaller group sizes does not necessarily diminish or negatively affect well-being (Neal Webb, Hau and Schapiro, 2019). Interestingly, a study investigating behavioural differences related to age of captive chimpanzees, highlights the importance of creating and sustaining compositionally diverse groups in captivity (Webb *et al.*, 2018). Housing aging populations of captive primates will be unavoidable for some species and that group demographics can have behavioural and welfare implications (Webb *et al.*, 2018).

A further consideration relates to the impact group size has on cognitive processes, and in particular the role of group size in the facilitation of social learning (Croney and Newberry, 2007). Inadequate group sizes can negatively affect the transmission of important adaptive behaviours, such as predator avoidance, tool use and cooperative behaviour in captivity, the significance of this could become apparent and affect the success of reintroductions in future conservation projects (Croney and Newberry, 2007). Group size could therefore contribute to the transgenerational effect associated with the loss of behaviours in captive settings unless husbandry practice including enrichment is used to mitigate the effects of captivity.

1.8.2 Husbandry considerations

The husbandry practices used with captive primates can have a significant impact on their behaviour (Ward, Sherwen and Clark, 2018). For example, inadequate or inappropriate husbandry practice can lead to stress and anxiety which in turn can lead to problematic behaviours such as aggression, self-injury, social withdrawal and other stereotypical behaviours (Rose, Nash and Riley, 2017). On the other hand, positive husbandry practice can promote mental and physical well-being, reduce stress and encourage natural behaviours (Bassett and Buchanan-Smith, 2007). One of the main challenges zoos face is the lack of standardised evidence-based animal welfare science at species level (Wolfensohn *et al.*, 2018). Aspects of husbandry practice and the potential impacts on behaviour, are considered in table 5, as well as possible solutions. Developing evidence-based, species level information that is shared throughout the zoo community, enables the identification of negative welfare impacts associated with husbandry practice (Bacon, 2018).

Rigorous, standardised husbandry would not be appropriate in all circumstances, and many factors restrict the use of some suggested best practices (Wolfensohn *et al.*, 2018). This is supported by Tuite *et al.,* (2022) who investigated the use of recommended enrichment practices in zoos, and concluded that conflicting priorities, uncertainty about effective practice and visitor perception were factors effecting implementation. However, zoos can use aspects of appropriate evidence-based approaches to inform evolving husbandry practices, that optimise the welfare of primates in captivity (Rose, Nash and Riley, 2017; Wolfensohn *et al.*, 2018). Whilst the scale of such collaboration is challenging, it is not necessarily impossible, as demonstrated by existing, successful captive breeding programmes managed by the zoo community.

Enrichment is an important part of primate husbandry practice, that can be used to mitigate the effects of captivity, support the behavioural needs and encourage the expression of species appropriate behaviour of captive primates (Coleman, Weed and Schapiro, 2013; Maple and Perdue, 2013; Sha *et al.*, 2016). Investigating the suitability of enrichment is therefore an important area of research in zoos.

Table 5: Suggested husbandry practices that potentially impact behaviour and possible solutions

Husbandry practice	**Possible impact on behaviour**	**Possible solution**	**Reference**
Predictable feeding routines	Boredom Anticipatory behaviour Stereotypical behaviour	Varied feeding times Novel feeding enrichment Cognitive enrichment	(Bassett and Buchanan-Smith, 2007)
Predictable feeding locations	Boredom Anticipatory behaviour Stereotypical behaviour	Hiding food in different locations Novel cognitive enrichment	(Bassett and Buchanan-Smith, 2007)
Processed food e.g. chopped fruits, shelled nuts	Lack of food manipulation and handling skills Lack of problem-solving skills Lack of tool use skills	Offering food in unprocessed form Enrichment that requires exploration and problem-solving	(Hosey, 2005)
Training	Stress Unnatural behaviour repertories Suppressed natural behaviours	Only use positive reinforcement Allow animals choice Encourage natural behaviour Use training as enrichment	(Ward and Melfi, 2013) (Melfi and Thomas, 2005)
Health Screening	Stress Fear	Positive reinforcement training	(Ward and Melfi, 2013) (Melfi and Thomas, 2005)
Controlled reproductive, maternal or paternal behaviour	Frustration Stereotypical behaviour Aggression Effects on social status Developmental issues	Reversible reproduction controls Appropriate grouping Close evaluation of controls Cognitive enrichment	(Bacon, 2018) (Wolfensohn and Honess, 2005) (Hosey, Melfi and Pankhurst, 2009)
Hand- rearing, early maternal separation when infant rejected by parent or at risk	Mal-imprinting Impaired cognitive development Maternal deprivation Stereotypical behaviour Impaired maternal competence	Minimise use of hand rearing Minimize human contact Cognitive enrichment to encourage cognitive development	(Bacon, 2018) (Nash *et al.*, 1999) (Morimura and Mori, 2010)
Human interactions Zoo staff Zoo visitors	Stress Stereotypical behaviour Habituation	Choice of enclosure use Off show areas Positive reinforcement training	(Gartner and Weiss, 2018)

1.9 Enrichment

Enrichment is the purposeful provision of stimuli, that elicits species specific behaviour and enhances welfare of captive animals (Tuite *et al.*, 2022).

1.9.1 Environmental enrichment

A generally agreed and widely cited definition for environmental enrichment acknowledges that enrichment should enhance animal welfare:

> "*…an animal husbandry principle that seeks to enhance the quality of captive animal care by providing the environmental stimuli necessary for optimal psychological and physiological well-being*" (Shepherdson, 1998, p. 1).

Whilst this definition places welfare at the core of environmental enrichment, evolving attitudes towards animal welfare and ethics sees enrichment practice vary considerably, from simplistic scatter feeding to complex problem solving tasks (Kim-McCormack, Smith and Behie, 2016). Environmental enrichment has become a mainstream husbandry practice in zoos, incorporating strategies to enhance the captive environment by providing stimuli which typically includes, for example: varied feeding methods, alterations to the physical environment and the addition of sensory stimulus (Figure 6), aimed at keeping animals occupied and increasing their ability to cope in their captive environment (Shepherdson, 2003). By increasing the level of stimulation and complexity of the captive environment species appropriate behaviours can be increased (Shepherdson, 2003). Some of the reported physiological and psychological welfare benefits of environmental enrichment include decreased morbidity and reduced stereotypical behaviour (Hall *et al.*, 2021). This is supported by research that reported frequent interaction with enrichment decreased stress and stereotypical behaviour in squirrel monkeys (*Saimiri sciureus)* (Sha *et al.*, 2012). Although environmental enrichment is now considered commonplace in zoos, most forms of enrichment used are rarely empirically evaluated or evidence-based (Shepherdson, 2003). This calls for further scientific study in order to advance our knowledge and improve the welfare of captive animals (Shepherdson, 2003). Many forms of environmental enrichment are designed to encourage captive animals to express natural behaviours, however, Hall *et al.,* (2021) propose that most enrichment, only provides basic cognitive challenge, and that more focus should be on developing enrichment that provides higher levels of cognitive stimuli.

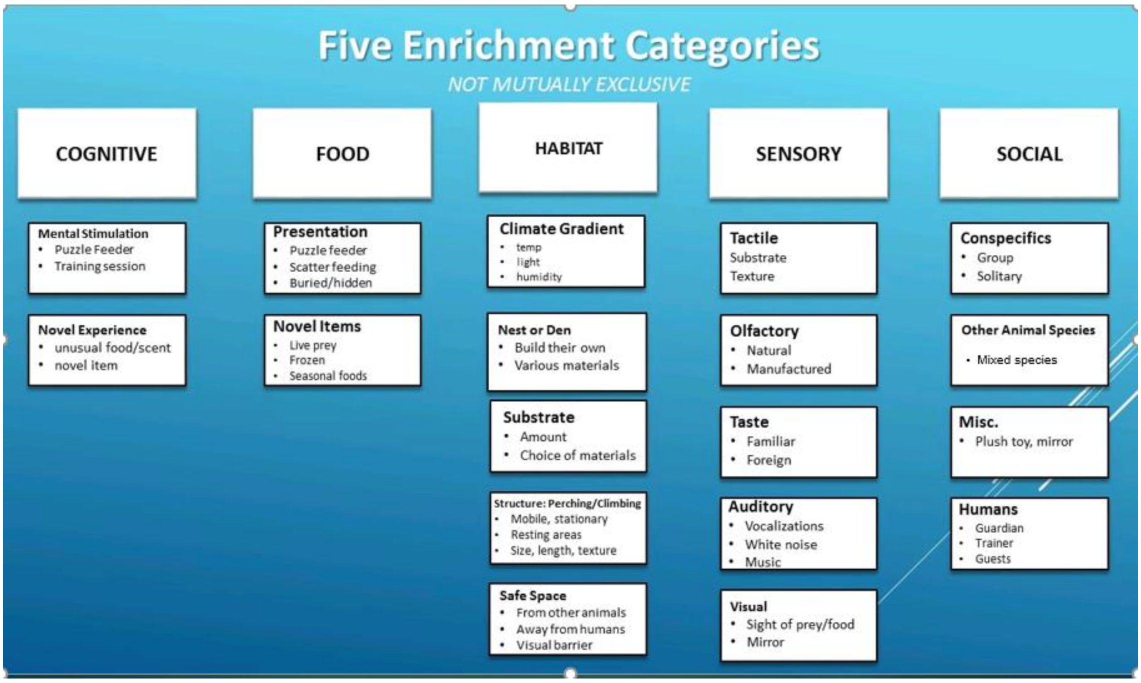

Figure 6: Enrichment categories (taken and modified from The Shape of Enrichment (2011)).

1.9.2 Cognitive enrichment

There is evidence to suggest that animals, when given a choice, will in some instances, actively seek a challenge (Spinka and Wemelsfelder, 2011). An example of this, includes a study of female long-tailed macaques (*Macaca fascicularis)* who reportedly favoured engaging in more complex challenging tasks despite being able to gain food rewards from more simple tasks (Watson, Shively and Voytko, 1999). The notion that animals seek and chose challenge, is supported by the phenomenon of contrafreeloading, whereby animals chose to work for a reward despite identical rewards being readily and easily available (Ogura, 2011; Clark, 2017). While explanations for contrafreeloading remain ambiguous, it is generally accepted that there is sufficient evidence to suggest that exploration and the acquisition of a resource is sometimes favoured over the resource itself (Clark, 2017). Research by Ogura (2011, p. 431) investigating contrafreeloading behaviour of Japanese macaques (*Macaca fuscata)* suggests that control over the environment acts as a motivating factor and that therefore, contrafreeloading behaviour is “self-reinforcing”. Thus, supporting the notion that animals in captivity need to be provided with the opportunity to control aspects of their environment and use complex cognitive skills, which can be facilitated through zoos using challenging novel cognitive enrichment (Meehan and Mench, 2007). This is further supported by Morimura, Hirata and Matsuzawa (2023), who as part of caring for captive Chimpanzees, link the need for cognitive challenges, specifically including daily decision making tasks with successful conservation of the species.

Research to review cognitive enrichment in practice, by Hall *et al.,* (2021), analysed the responses of 177 staff from captive animal facilities across the world. Their findings indicate that participants believe cognitive enrichment to be important for animal welfare, however, time constraints, financial investment and keeper interest were factors that affect the practice of cognitive enrichment. The study also reported a significant disparity in the use of cognitive enrichment, the most reported use of cognitive enrichment was with carnivores (76.3%) with fish and amphibians being largely overlooked (16.9%), primates were just below carnivores at 71.2% (Hall *et al.*, 2021). 54% of the respondents stated that primates were not receiving cognitive enrichment, but that they felt that they should. Therefore, despite the suggestion that there has been a bias towards primates in cognitive enrichment research, the use of cognitive enrichment in zoos is still lacking (Clark, 2017; Hall *et al.*, 2021). It is proposed that this is, in part, due to the perception that cognitive enrichment needs to be highly technical (Hall *et al.*, 2021) as well as practical limitations such as time, money and experience (Clegg *et al.*, 2023).

A meta-analysis of cognitive enrichment carried out in 2007, suggested that only 3% of zoo enrichment was cognitive, clearly this study was carried out sometime ago and the use of cognitive enrichment is likely to have increased, however there is a lack of up to date data to report (Clark, 2017). The limited use of cognitive enrichment, and therefore cognitive challenge in captivity, may contribute to short-term and long-term welfare implications, and especially for those species with higher cognitive function (Clark, 2011). Animals in captivity are not necessarily being provided with the appropriate opportunities to express complex natural behaviours, such as cooperative behaviour, which would form part of their wild activity budget (Clegg *et al.*, 2023). As part of a study by Swaisgood and Shepherdson (2005) they reported that although zoo enrichment is associated with a significant reduction in stereotypical behaviour, for most zoo species, there is a lack of published research scrutinising enrichment. In order to meet welfare standards, it is argued that zoos have a duty to ensure that captive environments provide sufficient cognitive challenge and therefore a scientific research approach to enrichment is necessary (Meehan and Mench, 2007).

1.9.3 Welfare benefits of cognitive enrichment

Primates have complex cognitive abilities, therefore, cognitive enrichment is considered an essential aspect of husbandry practice, that should be used to maintain and improve the welfare of captive primates (Hall *et al.*, 2021). Because captive environments are predominately constrained, predictable and lack challenge (Meehan and Mench, 2007; Clark, 2011), primates spend less time engaging in behaviours that require problem solving, decision making and social interaction. As a consequence, this can result in boredom, frustration, developing abnormal behaviours and the decline of cognitive function (Clark, 2011, 2017). Linked to the Five Domains Model (Figure 4) cognition is an important welfare consideration for captive primates. Zoos need to ensure that cognitive enrichment is evidence-based, and not only taxa specific, but also specific to the needs of individual groups housed, to ensure it is suitable and appropriate (Jacobson *et al.*, 2019). Appropriate cognitive enrichment can be used to enhance welfare by: providing mental stimulation; improving cognitive function; creating arousal; encouraging natural behaviours; facilitating choice and decision making; encouraging problem solving skills. As mentioned previously, achieving the correct level of challenge is essential if cognitive enrichment is to be effective, Meehan and Mench (2007) suggest that the level of challenge of a task should be balanced with the level of skill participants have to achieve an optimum result (Figure 7). This concept is supported by Lopresti-Goodman and Villatoro-Sorto (2023) who propose that primates respond with frustration if a challenge is too high, and individuals are unable to successfully complete cognitive enrichment tasks. Another point for consideration is that novel enrichment can become ineffective if the task does not provide optimum challenge and if primates become habituated to the novel device over time, resulting in decreased interaction and motivation (Clark *et al.*, 2019; Padrell *et al.*, 2022).

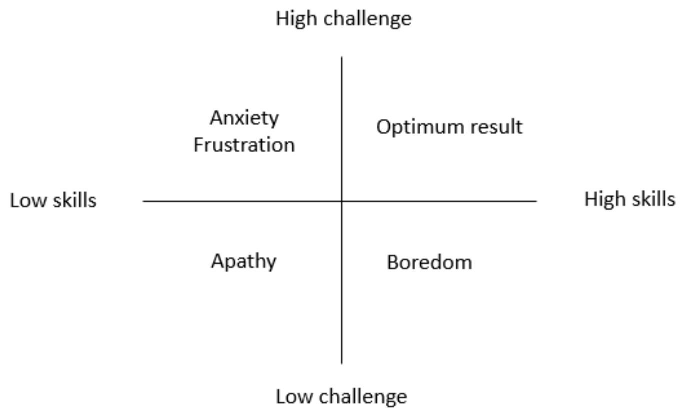

Figure 7: Four potential subjective states, in response to level of challenge of cognitive enrichment and the skill level of individuals (modified from Meehan and Mench 2007).

A study reviewing the suitability of a novel cognitive enrichment device for Western lowland gorillas (*Gorilla gorilla gorilla*) housed at Bristol Zoo proposed that despite only three out of the six individuals successfully solving the cognitive task, even unsuccessful individuals may have gained intrinsic benefits (Clark *et al.*, 2019). Researchers based this suggestion on unsuccessful individuals continuing to interact with the device and the lack of any negative welfare indicators (Clark *et al.*, 2019). What is apparent, is that optimum enrichment practice can only be established through research investigating the cognitive ability of captive primates.

Cooperative tasks as forms of cognitive enrichment can provide captive primates with the opportunity for additional social interaction by encouraging natural collaborative behaviour (Kemp, 2023). Cooperative interactions can facilitate social bonding in captive primates, reducing agonistic and stress related behaviours (Stocker *et al.*, 2020). In the wild cooperative anti-predator behaviour has been reported for both *M. nigra* (Micheletta *et al.*, 2012) and *C. capucinus* (Jack *et al.*, 2020). Despite the ecological validity, the simulation of cooperative anti-predator behaviour in a zoo setting raises a number of issues. Firstly, ethical concerns emerge regarding the potential induction of fear and anxiety in captive primates for research purposes. This requires careful consideration, as it involves balancing the scientific value of the research with the welfare of the animals. Secondly, zoos have the challenge of managing visitor experience, visitors to zoos often express concerns witnessing animals in a state of anxiety or fear and therefore, zoos have to strike a balance between the welfare of animals, visitor needs and research (Woods, 2002).

The benefits of cooperative puzzle based enrichment tasks include facilitating problem-solving, cognitive stimulation, explorative and social behaviours, whilst offering individuals choice and novel stimulus (Clark, 2017). Cooperative puzzle tasks are generally more acceptable to visitors in zoo settings and can be used as part of public education programmes (Clark, 2017). However, despite cooperative cognitive enrichment encompassing numerous potential welfare benefits, Kemp (2023) and Meehan and Mench (2007) imply it rarely forms part of mainstream enrichment practice for captive primates. Clark (2017) however, suggests that cognitive challenges are actively incorporated in enrichment practice but that scientific research assessing behavioural responses and welfare outcomes is lacking. Therefore, collaborative research is needed in zoos to investigate the effects of cooperative cognitive enrichment. Such research has the potential to inform species specific enrichment practice, which can be used to enhance the welfare of captive primates.

1.9.4 Conservation benefits of cognitive enrichment

It has been proposed that cognitive research in zoos is largely overlooked or neglected, with zoos focusing their time and efforts on conservation research (Hopper, 2017). It can be argued however that comparative cognitive research should and could be used to inform conservation research, to provide a deeper understanding of how cognitive mechanisms can affect, for example: how naïve captive animals respond to novel prey; foraging strategies; problem solving behaviour; novel objects; adaptability and tolerance of humans, all of which can further inform existing conservation strategies (Marzluff and Swift, 2017). This is supported by Riley (2018, p. 199) who argues that

> "*…if zoos are to improve their effectiveness at conservation they should consider the application of cognitive enrichment*".

Successful conservation management therefore, relies on multiple factors, historically animal behaviour is a field that has been principally overlooked and under-utilised as a conservation tool, despite evidence of its usefulness (Greggor *et al.*, 2016). Zoos are considered perfectly placed as one of the multiple stakeholders, in a position to contribute to conservation progress and innovation (Stadtländer, 2022). Where animals are considered critically endangered, it may be necessary in the future to reintroduce animals to the wild from captive populations (Gilbert *et al.*, 2017), the success of this will in part depend on the adaptability and cognitive skills animals possess, which are governed by the evolutionary history of the animal and their previous experience.

Research by Crates, Stojanovic and Heinsohn (2022), suggests that the selective pressures of captivity differ significantly from those in the wild and that genetic adaptions to captivity can occur over only a few generations. They propose that there are phenotype costs associated with captive breeding and reintroduction programmes, and a risk of introducing 'deleterious' alleles and pathogens, that can result in a loss of fitness in wild populations (Crates, Stojanovic and Heinsohn, 2022). The researchers argue that for captive breeding and reintroduction programmes to be successful, further research is needed to identify the various ways that captivity affects phenotypes, suggesting that more research is needed comparing the behaviour, morphology and health between wild and captive populations (Crates, Stojanovic and Heinsohn, 2022). By better understanding the effects of captivity, efforts can be made to control and reduce the associated phenotypic costs. Animals that do not encounter challenges in their environment are not provided with the opportunity to learn and adapt cognitive skills, which could be crucial for survival. The successful reintroduction of golden lion tamarins (*Leontopithecus rosalia*), has for example been attributed, in part, to the pre-release rehabilitation phase of the programme, which specifically included predator avoidance training (Beck *et al.*, 1991; Kierulff *et al.*, 2012). It is suggested that by incorporating cognitive enrichment within the husbandry management of zoo-housed primates, the need for intensive pre-lease rehabilitation training could be reduced.

Table 6 outlines example behaviour phenotypes that can affect the success of reintroduction programmes. In order to minimise phenotypic divergence between captive and wild populations and therefore increase the success of reintroduction programmes, further research is needed to inform ex-situ conservation management processes to include, exploring and assessing appropriate cognitive enrichment as part of captive husbandry management. A further benefit of ex-situ conservation research is to justify the significant costs associated with reintroduction programmes, investment is likely to decrease if programmes are unsuccessful. Therefore, using scientific research to advance and improve conservation management can also be used to encourage and secure funding and investment, which is vital for the survival of biodiversity (Crates, Stojanovic and Heinsohn, 2022).

Research investigating whether enrichment could be used to promote and stimulate foraging and locomotive behaviours for example, in captive bred golden lion tamarins, demonstrates the need to evaluate behavioural deficiencies in captive populations (Sanders and Fernandez, 2022). Ex-situ conservation programmes need to ensure that captive bred individuals, and future generations are equipped with the necessary survival skills, which can be achieved through mitigating any negative effects of captivity by providing opportunities for zoo-housed animals to express natural behaviours which should increase the success rate of reintroductions from zoo populations (Sanders and Fernandez, 2022). It is important to investigate the cognitive capabilities of zoo-housed primates, including their cooperative behaviour, to assess their suitability to be used in conservation breeding programmes and so that appropriate cognitive enrichment can be used to prevent the transgenerational loss of behaviours in captivity (Crates, Stojanovic and Heinsohn, 2022). Active participation in conservation research and management is likely to help zoos evolve and secure their futures (Rabb and Saunders, 2005).

Table 6: Behavioural phenotypic changes in captive animals (modified from Crates, Stojanovic and Heinsohn, (2022)).

Traits	**Indicators relative to wild conspecifics**	**Related aspects of animal husbandry**	**Related aspects of release protocols**
Behaviour:			
Vocalisations	Vocal complexity Repertoire Context specific	Opportunities to learn and refine vocalisations Social learning from conspecifics Presence of stimuli to evoke appropriate vocalisations	Selection of suitable individuals for release that produce and recognise appropriate vocalisations
Animal movement	Timing Direction Duration Location	Ability to exercise Ability to perform natural movement Ability to experience migratory cues	Social integration with experienced conspecifics Soft releases Timing and location of release
Sociality	Social connections Social cohesion Indication of neophobia, Boldness, exploratory behaviour	Opportunity to engage in social interactions Some autonomy over choice of social interactions and associations	Selection of suitable individuals for release Consideration of social structures Soft releases
Cognition	Behavioural flexibility in response to novelty Appropriate response to predators Food recognition Problem solving capacity Cooperative behaviour	Cognitive enrichment Stimulation Social learning Exposure to novelty Exposure to natural and novel foods Opportunity to make choices Opportunity to learn foraging, antipredator and cooperative behaviours	Cognitive testing Selection of suitable individuals for release Age of release cohort Pre-release training

1.10 Study Species - Sulawesi Black Crested Macaques (*Macaca nigra*)

M. nigra are a critically endangered species of macaque that inhabit the island of Sulawesi in Indonesia. They were last assessed for the IUCN Red List of Threatened Species in 2015, the main threats to this species were identified as habitat loss and poaching (SOS IUCN, 2023). Despite Indonesian laws prohibiting the hunting of this species and habitat destruction, it is estimated that the wild population of *M. nigra* has declined by over 80% since the 1990s (Hilser*et al.*, 2013), leaving approximately 4,000 – 6,000 wild individuals (Johnson *et al.*, 2020).

M. nigra are considered key to the North Sulawesi ecosystem and are therefore used as a flagship species to raise awareness of biodiversity conservation (Hilser *et al.*, 2013). As a critically endangered species, in-situ conservation efforts include a project implemented by Whitley Wildlife Trust (now Wild Planet Trust) between 2012-2015 which aimed to reduce injuries and mortalities of *M. nigra* due to illegal activities by 50% and to increase the effectiveness of the management of the endemic population (SOS IUCN, 2023). The Wild Planet Trust also established Selamatkan Yaki, which is an organisation that works with government officials and the people of Sulawesi, to develop strategies to protect the wild habitat of *M. nigra*. The Macaca Nigra Project, established in 2011, began as a scientific research programme investigating the biology and behaviour of *M. nigra,* and has since developed a conservation education programme in Tangkoko, North Sulawesi. The education programme of the project encourages positive attitudes and behaviour toward the local environment and critically endangered *M. nigra.* A recent review assessing the impact of the conservation education programme, reported that the programme has significantly increased school pupils knowledge and positive behaviour towards wildlife (Chanvin *et al.*, 2023). The review hopes to inspire similar and future conservation education programmes in Sulawesi (Chanvin *et al.*, 2023).

Research by Mittermeier *et al.,* (2007) suggested that the only remaining native genetically viable population of *M nigra* is within the Tangkoko Reserve, found on the north-eastern coast of Sulawesi. Their research raised concerns regarding the continued and projected decline of *M. nigra,* endangering the genetic diversity and therefore survival of this wild population (Mittermeier *et al.*, 2007). It is suggested that an up to date assessment of the overall population in Sulawesi is urgently needed to help inform existing and future conservation strategies, both within and outside of the Tangkoko Reserve. A non-native population have also been reported on the island of Bacan in the North Maluku archipelago, this population is thought to be less threatened however, further research is needed to fully assess the viability of using this population for conservation purposes (Hilser *et al.*, 2013). Thus, with a reported decreasing native population trend (IUCN, 2022) and without an up to date assessment of all wild populations, it is considered essential that ex-situ conservation is used to protect and preserve this species. Current European ex-situ conservation of *M. nigra,* is currently managed by The Wild Planet Trust through an EAZA Endangered Species Programme (EEP, EAZA 2023).

M. nigra are diurnal, semi-terrestrial primates, spending approximately 60% of their day on the forest ground. Their diet is primarily frugivorous, supplemented with plants, invertebrates and vertebrates available in their natural forest habitat (IUCN, 2022). In the wild, *M. nigra* live in large multi-male multi-female groups with female philopatry and male dispersal upon sexual and physical maturity (Duboscq *et al.*, 2013). Average group size is believed to be 70 individuals (Micheletta, 2012), this is significantly larger than the average group size of other macaque species and may be attributed to social tolerance (Thierry, 2000, 2007). Captive groups housed in zoo collections are generally considerably smaller than wild groups. Despite being considered one of the most tolerant macaque species, the social organisation of *M. nigra* is determined by linear dominance hierarchies (Thierry, 2007). Male dominance rank is determined by direction of displacement, the frequency of grooming a male receives from females and the amount of time females spend in proximity to a male (Reed, O'Brien and Kinnaird, 1997). Hierarchies significantly influence the social interactions of males, who fiercely compete for alpha male status (Marty *et al.*, 2017). Female rank is organised by matrilineal dominance hierarchies (Duboscq *et al.*, 2017), female social interactions are bi-directional and they display high levels of reconciliatory behaviour and social tolerance (Duboscq *et al.*, 2013). In captivity, female grooming behaviour can be explained by direct reciprocity, which is independent from kinship and rank (Dunayer *et al.*, 2019). Although *M. nigra* live in cohesive social groups in the wild, competition for resources can result in aggression, however, it is suggested that conflict is often quickly escaped and diffused (Petit, Abegg and Thierry, 2017; Cowl, Walker and Shultz, 2021). In captivity, aggressive interactions can escalate, as a consequence of not being able to escape conflict situations, higher frequencies of social interactions are reported and dominant individuals easily control access to resources (Cowl, Walker and Shultz, 2021). There are health and welfare risks associated with aggression, and therefore in captive settings, group size, group composition and resource provision are actively managed to minimise aggression (Cowl, Walker and Shultz, 2021).

The high level of social tolerance and complex social interactions of *M. nigra* make them interesting subjects for behavioural studies. In the wild, males form cooperative coalitions to compete for and defend dominance status, strong competition can constrain affiliative and cooperative behaviour, which is therefore more prevalent in females (Tyrrell *et al.*, 2020; Duboscq and Micheletta, 2023). Intergroup cooperation is used to defend food resources (Martínez-Íñigo *et al.*, 2023) and for predator defence (Micheletta *et al.*, 2012). Despite evidence that *M. nigra* display varying forms and levels of cooperative behaviour in the wild (Micheletta *et al.*, 2012; Martínez-Íñigo *et al.*, 2021) I have not found any research investigating the use of novel enrichment to encourage cooperative behaviour of *M. nigra* in captivity. It is hoped that this study can be used to inform husbandry practice.

1.11 Study Species – Columbian White-throated capuchins (*Cebus capucinus*)

C. capucinus are a New World monkey ranging from Honduras to Panama in Central America and along the west of the Colombian Andes to Ecuador in South America (Tórrez-Herrera, Davis and Crofoot, 2020). Most recently assessed as 'vulnerable' in 2020 by the IUCN Red List of Threatened Species, the main threats to this species were identified as habitat degradation and the pet trade (IUCN, 2022). There is currently no population data for this species however, the IUCN has inferred a 30% reduction in numbers over the course of the last three generations (IUCN, 2022). The captive breeding of *C. capucinus* is manged by La Vallée des Singes zoo in France. With the recent re-categorisation of this species from least concern to vulnerable in the wild, both in-situ and ex-situ conservation efforts will need to escalate in order to protect this species.

C. capucinus are diurnal, arboreal primates (Rose and Fedigan, 1995) that spend approximately 50% of the day foraging (Mittermeier et al., 2013). *C. capucinus* home ranges are between 80 and 150 hectares (Tórrez-Herrera, Davis and Crofoot, 2020) they can forage over distances of up to three kilometres a day. They are omnivorous, their diet includes a wide variety of fruits, seeds, arthropods, nestlings, small mammals and reptiles (Tórrez-Herrera, Davis and Crofoot, 2020; IUCN, 2022).

C. capucinus are gregarious, and in the wild live in large multi-male, multi-female social groups, typically consisting of 10-30 individuals led by a dominant male, with female philopatry and male dispersal (Jack and Fedigan, 2004; Perry, 2011). There are large variations in the length of male residency in natal groups, the average age of male dispersal is 4.5 years (Muniz *et al.*, 2010; Jack, Sheller and Fedigan, 2012). Alpha male tenures can be long lasting (Muniz *et al.*, 2010), other males within the group defer to the alpha male (Perry, 1998) and females spend more time in proximity with alpha males than other males within the group (Perry, 1997). Females have a reproductive interest in helping an alpha male maintain his dominant status, reducing the risk of infanticide and increasing their reproductive success (Perry, 1997). Cooperative food sharing behaviour is predominately associated with maternal kin-biases (De Aquino *et al.*, 2022). *C. capucinus* form strong coalitions which are important for maximising fitness (Perry, 2012). Male coalitions are beneficial in terms of reproductive dominance, inter-group dominance and predator defence (Muniz *et al.*, 2010; Perry, 2012).

Schoof and Jack (2014) suggest that males form strong, reciprocal social bonds which are influenced by kin-bias. Research investigating aggressive coalitions of *C. capucinus*, suggests that individuals preferentially choose to form coalitions with higher ranking individuals, and with individuals that display high levels of affiliative and cooperative behaviour (Perry, Barrett and Manson, 2004). Female-female coalitions are formed to protect against aggressive males and defend resources in the wild (Perry, 1997). Hemelrijk and Steinhauser (2007) suggest cooperative behaviour can be influenced by group size, composition and resource distribution, all aspects that are managed and controlled in captivity. The group size and composition (see methods 2.2.1) of the captive group of *C. capucinus* used in this study are significantly different to that observed in the wild and it is acknowledged that this could be a limitation of the study.

The complex social behaviours of *C. capucinus* make them interesting study subjects. The ability of wild *C. capucinus* to form cooperative alliances is considered a selective pressure in their evoluntionary history (Perry, 2012). In the wild, cooperation in this species is vital in relation to defence of resources, access to mates and caring for offspring, therefore making them an appropriate taxon for studying cooperative behaviour (Perry, 2012). This research will investigate the response of a captive group of *C. capucinus to* a novel cooperative enrichment task. It is hoped that this study can be used to inform husbandry practice.

1.12 Project aims

Current environmental enrichment efforts focus on promoting natural behaviours, but they often fall short in providing adequate cognitive stimulation (Hall *et al.*, 2021). This study introduces cooperative enrichment devices specifically designed to offer high levels of cognitive stimuli. The overarching aim of this study is to investigate the behavioural responses of captive *M. nigra* and *C. capuchinus* to a novel cooperative enrichment device. The study has specific objectives, including assessing the spontaneous cooperative abilities of both species in a captive environment without prior training or habituation to the device, and evaluating the suitability of the devices as forms of cognitive enrichment. Therefore, the aims include identifying the impact of the device on activity budgets, exploring levels of interaction throughout the duration of the study and examining factors such as gender differences. The study aims to contribute to the understanding of the effects of novel cognitive enrichment devices on captive primate behaviour and welfare.

1.12.1 Objectives and predictions relating to both case study 1 (M. nigra) and case study 2 (C. capucinus)

1. To evaluate if the captive groups at Newquay Zoo can cooperate to solve a novel cooperative enrichment task to gain a food reward, without prior training.

   Prediction: The captive groups will not successfully cooperative to gain a food reward without prior training. Previous pulling paradigm research suggests training will be required.

2. To assess if the device affects the activity budget of either captive *M. nigra or C. capuchinus.*

   Prediction: Novel enrichment will increase the expression of prosocial behaviour because cooperation and cooperative tasks strengthen social bonds by promoting engagement. The proportion of time spent locomoting will also increase due to the device acting as an incentive to actively engage and stimulating exploratory behaviour. It is predicted that aggression between conspecifics will decrease when the device is present by promoting and stimulating social interactions and preventing boredom.

3. To evaluate if there is a difference in behavioural interactions with the device and the latency to approach the device between individual subjects.

   Prediction: There will be a difference in the use of the novel cooperative enrichment between individual subjects. Including latency to approach the device, the time spent interacting with the device, the number of approaches with contact, aggressive acts towards the device and number of rope-pulls.

4. To evaluate if there is a difference in response to the device between females and males.

   Prediction: There will be a difference in the behaviour between female and male subjects, with males approaching the device more frequently, interacting with the device longer and showing higher levels of aggression directed at the device. It is also predicted that females will have higher latency to approach the device, due to males monopolising the device.

5. To determine if there is a linear relationship between the number of trials and the time spent interacting with the device.

   Prediction: There will be a negative linear relationship, time spent interacting with the device will decrease over the number of trials due to habituation to the novel device.

6. To determine if there is a linear relationship between the number of trials and the number of rope-pulls.

   Hypothesis: There will be a negative linear relationship, the number of rope-pulls will decrease over the number of trials due to habituation to the novel device.

7. To determine if there is a linear relationship between the number of trials and latency to approach the novel cooperative enrichment device.

   Hypothesis: There will be a negative linear relationship, latency to approach the device will decrease over the number of trials.

1.12.2 Objectives and predictions– Case study 1 *M. nigra*

8. To determine if there is a linear relationship between the number of trials and the number of aggressive acts directed at the device.

   Prediction: There will be a negative linear relationship, the number of aggressive acts directed at the device will decrease over the number of trials due to habituation to the device. If the primates are able to successfully cooperate to gain a food reward, aggression directed at the device is predicted to decrease.

9. To determine if there is a linear relationship between the number of trials and the number of approaches with contact to the device.

Prediction: There will be a negative linear relationship, the number of approaches will decrease over the number of trials due to habituation to the novel device.

10. To evaluate if there is a difference in the number of rope-pulls during a dyadic interaction at the device, compared to the number of rope-pulls when an individual is alone at the device linked to presence-dependent cooperation.

    Prediction: There will be a higher number of rope-pulls when individuals are in the presence of others as the action of pulling will attract others to the device (linked to presence-dependent cooperation).

11. To evaluate if frequency of interactions at the device, is associated with levels of relatedness.

    Hypothesis: There will be a higher number of interactions at the device between individuals with a relatedness coefficient of 0.25 and above.

1.12.3 Objectives and predictions – Case study 2 C. capucinus

12. To evaluate if there is a difference in response to the device between adults and juveniles.

    Prediction: There will a difference in the behaviour between adult and juvenile subjects, with adults interacting with the device and accessing food from the device more frequently. Based on research suggesting adults perform better because they are more cognitively developed.

13. To determine if there is a linear relationship between the number of trials and the proportion of time spent in proximity to the device.

    Prediction: There will be a negative linear relationship, time spent in proximity to the device will decrease over the number of trials due to habituation to the novel device.

14. To evaluate if there is a difference in the latency to approach the enrichment device, between adults and juvenile subjects.

    Hypothesis: Juveniles will have higher latency to approach the device due to adult subjects monopolising the device.

2. Methodology

2.1 Case study 1 - *M. nigra*

2.1.1 Subjects and housing

The study subjects were a social group of seven, captive born *M. nigra* housed at Newquay Zoo, Cornwall. The group detailed in table 7, included adult and juvenile males and females. At the time of the study, this was a non-breeding group, with females having contraceptive implants as part of the EAZA Endangered Species Programme recommendations. The housing management consisted of two indoor and one outdoor enclosure areas (Figure 12), with individuals having access to all of the areas during the study. The subjects received no prior training or training during the study. All subjects were free to interact and access the enrichment device for the recorded observation periods. All subjects had free partner choice throughout.

Table 7: Summary of M. nigra subjects included within the study (information provided by primate keepers at Newquay Zoo).

Black Crested Macaque (*Macca nigra*)	Sex	Age (years)
Cheeketo	Male	18
Elvis	Male	7
Raffiki	Male	4
Maggie	Female	15
Solina	Female	14
Theo	Female	9
Kasih	Female	6

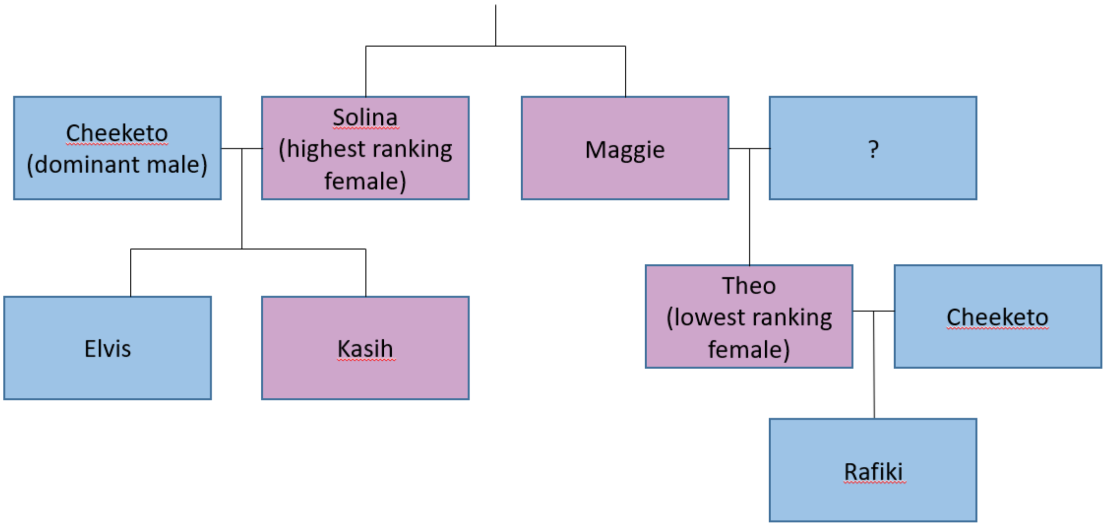

Figure 8: Family tree of captive M. nigra subjects (blue = male, pink = female, the? represents an unknown individual with whom Maggie mated with before she was relocated to Newquay Zoo).

2.1.2 Cooperative enrichment device

A novel cooperation enrichment device measuring 61 x 49cm, comprises a counter-sprung sliding tray within an outer box. The counter springs ensure that the tray only slides forward and dispenses a food reward when both ropes were pulled simultaneously. If one individual pulls alone, the counter springs prevent the tray from sliding forward. Ropes, attached to the sliding tray, pass through metal poles arranged at different length so that the ends of the rope are positioned beyond the reach of an individual *M. nigra,* to prevent an individual successfully sliding the tray and accessing a food reward alone (Figure 9). The poles are presented through existing training holes in an indoor mesh door as illustrated in figures 10 and 11. A section of the sliding tray is filled with food, and is clearly visible to the subjects. The device is designed so that two or more individuals need to simultaneously pull the rope to obtain a food reward.

Figure 9: Photograph of cooperative enrichment device (Sullivan, 2017).

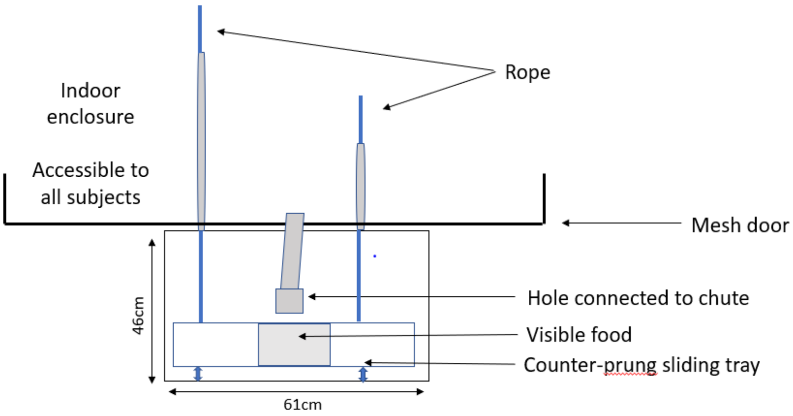

Figure 10: Aerial diagram of the device, illustrating a counter-sprung sliding tray within the main box. Attached to the sliding tray was rope thread through different length metal poles. The visible middle chamber of the sliding tray was baited with favoured nuts. To successfully access the food reward, two or more individuals needed to pull both ropes simultaneously so that the tray containing the food moved over the hole, through which food would be dispensed down a chute for the M. nigra to access.

Figure 11: Photograph of cooperative enrichment device in-situ at Newquay Zoo macaque enclosure (Sullivan 2017).

2.1.3 Overview of observations

To evaluate the impact of the device on the overall activity budget of the subjects, I used instantaneous focal sampling, the methods for this are explained in 2.1.4. Separate video recording equipment captured interactions with the device, these methods are described in 2.1.5.

2.1.4 Data collection schedule for activity budget analysis

I recorded all state behaviours by conducting focal observations using instantaneous sampling every 30 seconds (Martin and Bateson, 2007). I conducted behavioural observations in two conditions: when the device was present and when it was not, observing each subject for 10 minutes during each observation period. These procedures align with those used in previous captive primate behaviour studies (Jacobson *et al.*, 2019; Woods, Ross and Cronin, 2019; Padrell *et al.*, 2022).

I used focal observations to establish an activity budget for each individual subject. This approach allowed me to use individual responses to evaluate the suitability of the enrichment device, which is a suggested approach (Padrell et al. 2022). The collected data enabled me to calculate the proportion of time individual subjects spent performing behaviours during each observation period. Appendix 1 includes an ethogram for reference.

I randomised observations on different days between April and July at various times between 10:00 to 16:00. This diverse timing aimed to equally represent different times of the day and prevent any specific time from influencing behaviour. Subject order was randomised to minimise the impact of confounding variables related to presentation order. The observer's position is indicated on the enclosure diagram, as shown in Figure 12.

I presented the device to the macaques in a ground-level area of the indoor enclosure, indicated in figure 12.

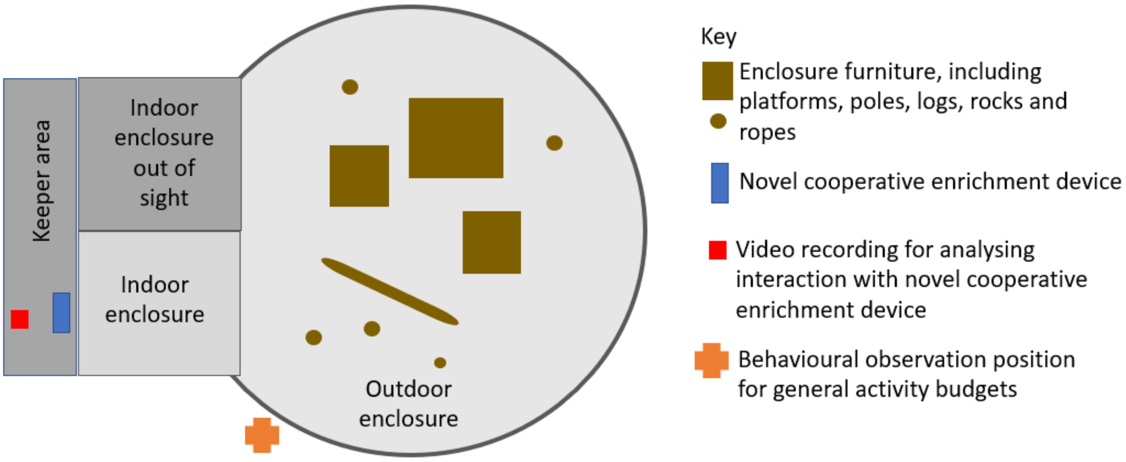

Figure 12: Diagram of M. nigra enclosure at Newquay Zoo

2.1.5 Video analysis

I recorded behaviour using a Panasonic LUMIX GH5s. I positioned the camera on a tripod behind the mesh door, within the keeper section of the indoor enclosure facing towards the indoor enclosure (Figure 13). The camera was switched on during presentation of the cooperative enrichment device and left to record footage until I uninstalled the device 70 minutes later. I stored the data on SD cards and later downloaded it to a hard drive.

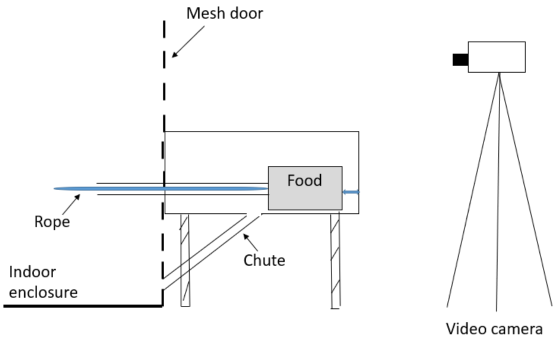

Figure 13: Side elevation of macaque cooperative enrichment device, demonstrating installation and video recording setup.

I utilised video analysis to record the following: a) individual latency, comparing the time (s) it took individuals to approach the device in each trial; b) time each subject spent interacting with the device (determined as individuals touching, exploring, sitting on the poles of the device); c) the number of times each individual approached and were within one metre of with the device; d) the number of rope-pulls for each subject, e) the number of aggressive behaviours directed at the device for each subject; f) dyad information engaging with cooperative enrichment device; g) whether the frequency of dyad interactions is associated with levels of relatedness.

I recorded dyads engaging at the enrichment device using an interaction matrix that identified the individual initiating the dyad (initiator defined as an individual who is first at the device) and a joiner (defined as an individual that joined another at the device) (definitions available in Appendix 2).

I calculated levels of relatedness using Hamilton's coefficient of relatedness (Figure 14).

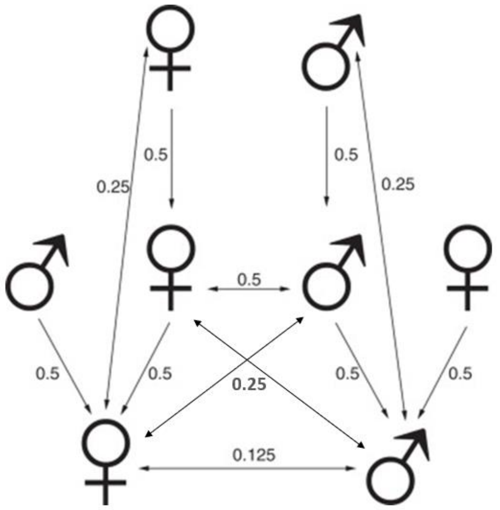

Figure 14:The coefficient of relatedness. In diploid organisms, every parent (top row) transmits 50% of its genetic information to each offspring (middle row). On the average, siblings therefore share half of each parent's contribution to their genome, adding to a coefficient of relatedness r *= 0.5. Consequently, cousins share* r *= 0.125 (bottom row). Likewise, these cousins are related to their common grandparents by* r *= 0.25 (modified from Brembs* (2013)*, relatedness coefficients between uncles/aunts and nieces/nephews, r = 0.25 added, as relevant for M. nigra subjects.*

2.2 Case study 2 – *C. capucinus*

2.2.1 Subjects and housing

The study subjects were a social group of five, captive born *C. capucinus* housed at Newquay Zoo, Cornwall. The group, included a breeding adult male and female, two juvenile males and a baby born at the beginning of the experiment, with details outlined in table 8. The housing management comprised one indoor and two outdoor enclosure areas, with individuals having access to all of the areas during the study.

The subjects received no prior training or training during the study. All subjects were free to interact and access the enrichment device for the recorded observation periods, maintaining free partner choice throughout.

Table 8: Summary of C. capucinus subjects included within the study (information provided by primate keepers at Newquay Zoo).

White-throated capuchin (*Cebus capucinus*)	Sex	Age (years)
Zaito	Male	14
Baru	Male	3
Diego	Male	1
Irazu	Female	16
New born	Unknown	Born 07/03/23

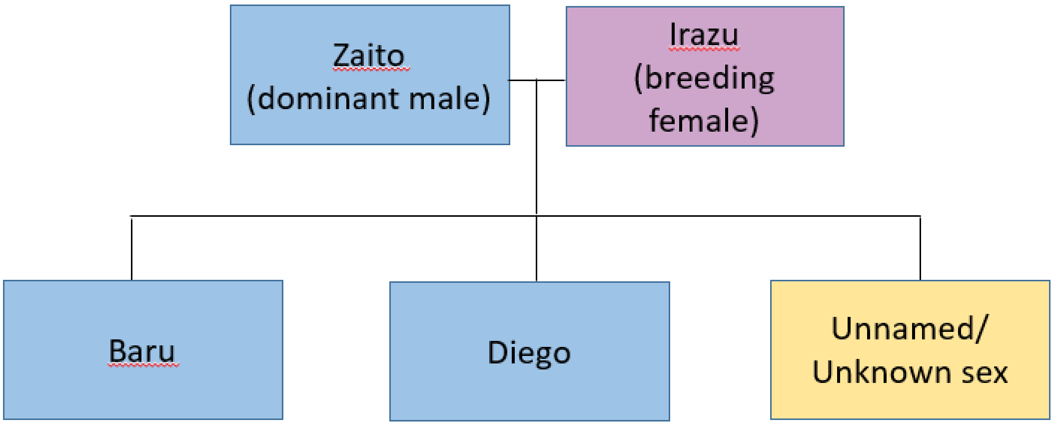

Figure 15: Family tree of captive C. capucinus subjects (blue = male, pink = female, yellow = unknown sex).

2.2.2 Cooperative enrichment device

I placed the device, measuring 1m x 20cm on the outside of the enclosure with the ends of the rope position through the mesh wall into the enclosure. The device had a countersunk hole to hold the food reward and was designed so that if only one end of the rope was pulled, the rope would slide through the eyelets.

Figure 16: Photograph of cooperative enrichment device (Sullivan 2023).

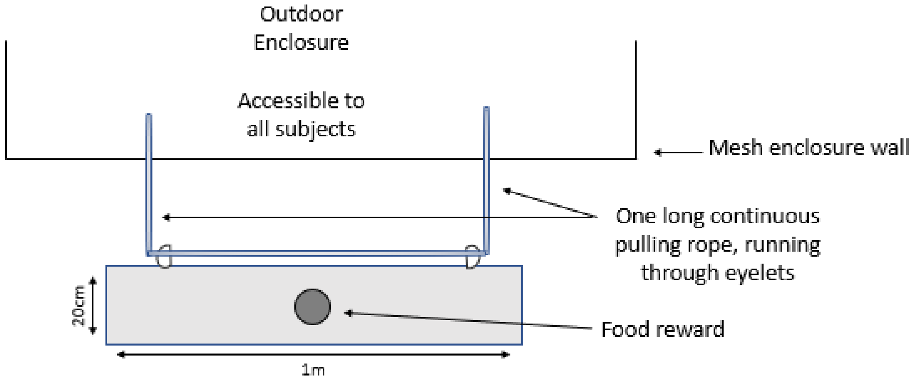

Figure 17: Aerial diagram of the device setup. The distance between the two rope ends was designed to be too long for one individual to be able to pull simultaneously. Therefore, the aim was that two or more individuals would need to pull together to slide the device close enough to access the food reward in the centre.

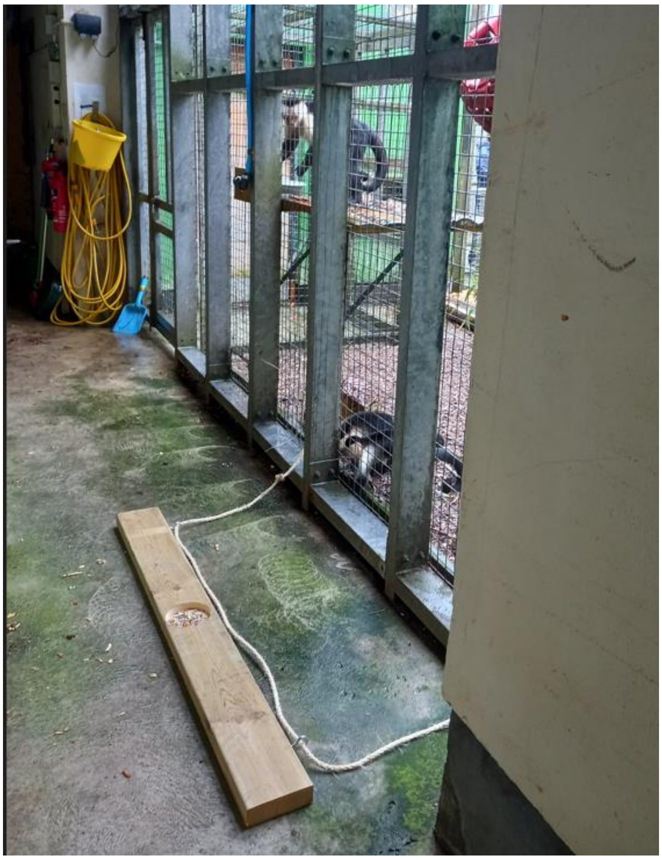

Figure 18: Photograph of cooperative enrichment device in-situ at Newquay Zoo capuchin enclosure (Sullivan 2023).

2.2.3 Overview of observations

I used two distinct methods of observation. 1) to collect data for activity budget analysis, the methods for this are explained in 2.2.4. 2) Separate video recording equipment to analyse interactions with the device, these methods are described in 2.2.5.

2.2.4 Data collection schedule

I recorded all state behaviours using the same focal instantaneous sampling methods as outlined in 2.1.4. An ethogram for case study 2 can be found in Appendix 3. I carried out observations on nine days when the device was present and ten days when the device was not present. Observations took place at varying times of the day between 10:00 and 16:00. Observations were randomised on different days between March and April and subject order was randomised to minimise the effect of confounding variables. Observers position is indicated on the enclosure diagram, Figure 19. I presented the device to the capuchins in a ground-level area of their outdoor enclosure, out of sight of visitors.

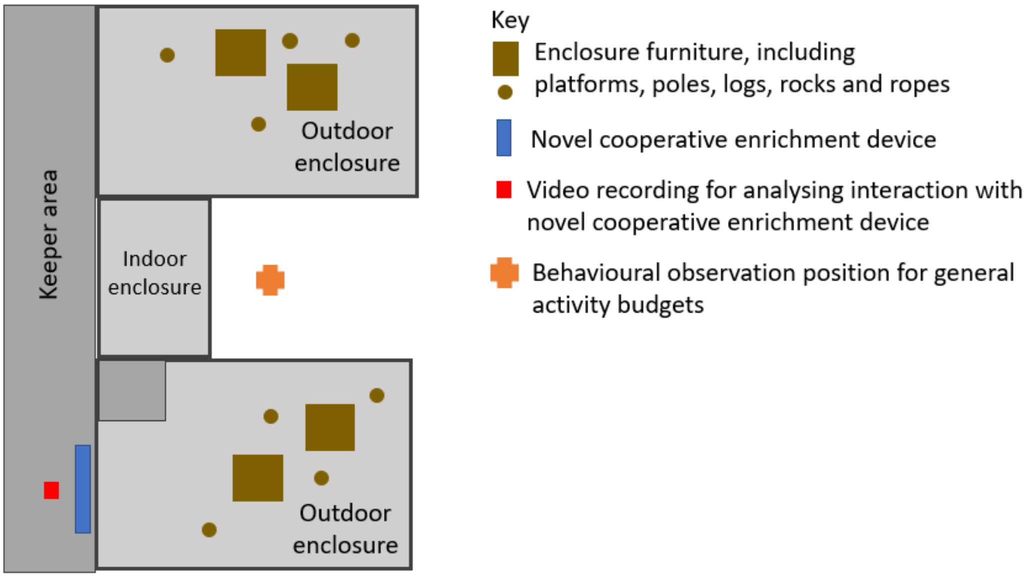

Figure 19: Diagram of C. capucinus enclosure at Newquay Zoo

2.2.5 Video analysis

I captured behaviour using a GoPro Hero 9. I positioned the camera within the keeper section of the indoor enclosure facing towards the device and the enclosure (Figure 20). The camera was switched on during presentation of the cooperative enrichment device and left to record footage until I uninstalled the device 40 minutes later. I stored data on an SD cards and later downloaded it to a hard drive.

I utilised video analysis to record: a) individual latency to approach the device; b) proportion of time individuals spent in proximity to the device (proximity was determined as an individual being within 1m of the device); c) proportion of time individuals spent interacting with the device (interaction was determined as touching the device); d) number of rope-pulls for each subject, e) number of times individuals accessed food from the device (definitions available in Appendix 4).

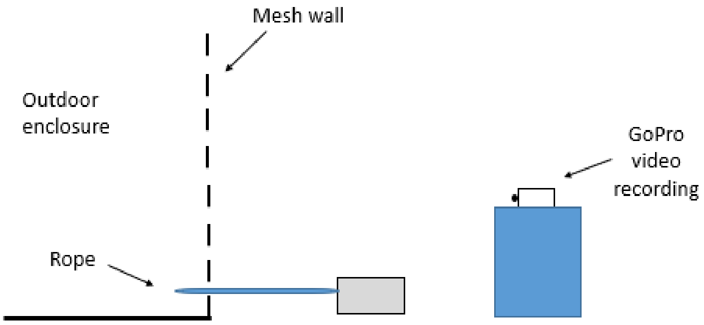

Figure 20: Side elevation of capuchin cooperative enrichment device, demonstrating installation and video recording setup.

2.3 Analysis

An overview of analysis is available in table 9.

2.3.1 Case study 1 – *M. nigra* activity budget data

I used observed data to calculate the proportion of time spent performing each behaviour, this was used for analysis. Due to the small sample size, the use of proportional data and following examination of the dispersion parameter, I used Quasibinomial generalised linear models (GLMs) to examine the effect of independent variables: condition (no cooperative enrichment device vs. cooperative enrichment device) and individual on the dependent variable: proportion of time expressing behaviour. All models treated condition (no cooperative enrichment device vs. cooperative enrichment device) and individual as fixed factors. The Drop model1 (Chi squared refinement) function determined the minimum adequate model to describe the data. I conducted analysis using R (Version 4.2.0), setting significance values at *p* <0.05.

2.3.2 Case study 1 – *M. nigra* video analysis

Since the data exhibited non-normal distribution, I employed non-parametric Kruskal-Wallis analysis to statistically analyse the difference between the individual macaques for: a) time spent interacting with the device b) the number of times each individual approached the device; d) number of rope-pulls, e) number of aggressive behaviours directed at the device. Additionally, Kruskal-Wallis tests were utilised to analyse any difference between female and male subjects for the aforementioned behaviours. Post-hoc analysis involved conducting pairwise Wilcoxon test. Analyses were performed using R (Version 4.2.0), with significance values set at *p* <0.05.

I assessed latency by comparing the time (s) it took for each individual to approach the device in each trial. Two macaques, Maggie and Kashi each received a maximum latency of 4200 (s) for nine trials, because they did not approach the device during those trials. I analysed latency using a non-parametric Kruskal-Wallis test in R (Version 4.2.0).

I used non-parametric, Spearman's Rank Correlations in R (Version 4.2.0 to determine linear relationships between trial number (1-10) and: 1) the amount of time (s) all individuals in the group spent interacting with the device; 2) the total number of aggressive acts directed at the device; 3) the total number of approaches with contact for all individuals; 4) the total number of rope-pulls for all individuals and 5) total group latency (s) to approach the device for each of the ten trials.

I used Gephi 0.10 network analysis to visualise the number of and direction of social interactions between individual *M. nigra* at the device. Data from an interaction matrix identified the individual first to approach the device = 'initiator' and individuals that joined them at the device = 'joiner'.

To analyse the relationships between relatedness coefficients and the frequency of interactions of subjects, I used Chi-Squared in R (Version 4.2.0).

2.3.3 Case study 2 – *C. capucinus* activity budget data

I calculated and analysed the proportion of time spent performing each behaviour from the observed data. Using Quasibinomial generalised linear models (GLMs) I investigated the effect of independent variables: condition (no cooperative enrichment device vs. cooperative enrichment device) and individual on the dependent variable: proportion of time expressing behaviour. The use of Quasibinomial GLMs was determined by proportional data, the small sample size and following the examination of dispersion parameters.

All models, included condition (no cooperative enrichment device vs. cooperative enrichment device) and individual as fixed factors. To determine the minimum adequate model to describe the data, I applied the Drop model1 (Chi squared refinement) function. The analysis were conducted using R (Version 4.2.0), with significance values set at $p < 0.05$.

2.3.4 Case study 2 – *C. capucinus* video analysis

I used non-parametric Kruskal-Wallis tests to analyse statistically significant differences between the capuchin subjects for: a) the time they spent in proximity to the device; b) the time they spent interacting with the device; c) the number of times they accessed food from the device; d) the number of rope-pulls and e) latency to approach the device in each trial. The analysis were conducted using R (Version 4.2.0), with significance values set at $p < 0.05$.

I also used non-parametric Kruskal-Wallis tests to analyse any differences between adult and juvenile subjects for all of the behaviours outlined above. The Analysis were conducted using R (Version 4.2.0), with significance values set at $p < 0.05$.

To determine linear relationships between trial number (1-9) and: 1) the proportion of time (s) the group spent in proximity to the device; 2) the proportion of time (s) the group spent interacting with the device; 3) the number of times subjects accessed food from the device; 4) the number of rope-pulls and 5) latency (s) to approach the device over the nine trials, I used non-parametric Spearman's Rank Correlations in R (Version 4.2.0).

Table 9: An overview of the behaviours recorded per species and inferential statistics performed

Species	**Behavioural observations: Behaviours on which Quasibinomial General Linear Models were preformed + Drop Model 1 Chi Squared refinement**	**Video Analysis: Shapiro normality test Kruskal-Wallis and Pairwise Wilcoxon Rank Sum Test**	**Video Analysis: Shapiro normality test Spearman Rank Correlation**	**iGraph Adjacency matrix Gephi network analysis**	**Chi-squared**
M. nigra	Locomotion, prosocial, foraging and feeding, aggression, alert, out of sight (Appendix 1)	Time spent interacting with the device, Number of aggressive acts directed towards the device, Number of approaches to the device, Number of rope-pulls, Latency to approach the device, Differences between male and female subjects (Appendix 2)	Time spent interacting with the device, aggression, number of approaches, number of rope-pulls and latency over the trials	Interaction matrix of individuals at the cooperative enrichment device	Relatedness coefficients and number of interactions at the cooperative enrichment device Solitary and social rope-pulls
C. capucinus	Locomotion, foraging and feeding, interaction with environmental enrichment, prosocial, solitary, aggression, out of sight (Appendix 3)	Proportion of time in proximity to the device, Proportion of time interacting with the device, Number of rope-pulls, Number of times accessed food from the device Latency to approach the device (Appendix 4)	Time spent in proximity to the device, time spent interacting with the device, number of rope-pulls, number of times food accessed and latency over the trials	Not included in the study due to lack of dyad interactions at the device.	Not included in the study. Due to family grouping, there was not enough variation in relatedness coefficients for analysis

3. Results

3.1 Case study 1 – *M. nigra* activity budgets

The Drop 1 Chi Squared function examined the significance of removing each main effect or interaction from the original model. These results are reported in Table 10.

In all of the overall quasibinomial GLM models, there was no significant effect of the condition: no cooperative enrichment device vs. cooperative enrichment device, on the proportion of time subjects spent performing any of the behaviours (Table 10 and Figure 21).

Table 10: Quasibinomial GLM models, including model refinement

Behaviour	Independent variables	Deviance	Drop 1 Chi Squared p value
Locomotion	Box	19.46	0.42
	Macaque	21.18	<0.05
	Box : Macaque	19.39	0.065
Prosocial	Box	64.14	0.47
	Macaque	67.63	0.25
	Box : Macaque	63.89	0.75
Aggression	Box	12.07	0.44
	Macaque	14.81	<0.05
	Box : Macaque	11.94	0.08
Alert	Box	33.57	0.26
	Macaque	36.42	<0.05
	Box : Macaque	33.27	0.24
Forage and feeding	Box	46.18	0.89
	Macaque	48.81	0.22
	Box : Macaque	46.11	0.15
Out of sight	Box	23.45	0.10
	Macaque	23.97	0.48
	Box : Macaque	22.96	<0.05

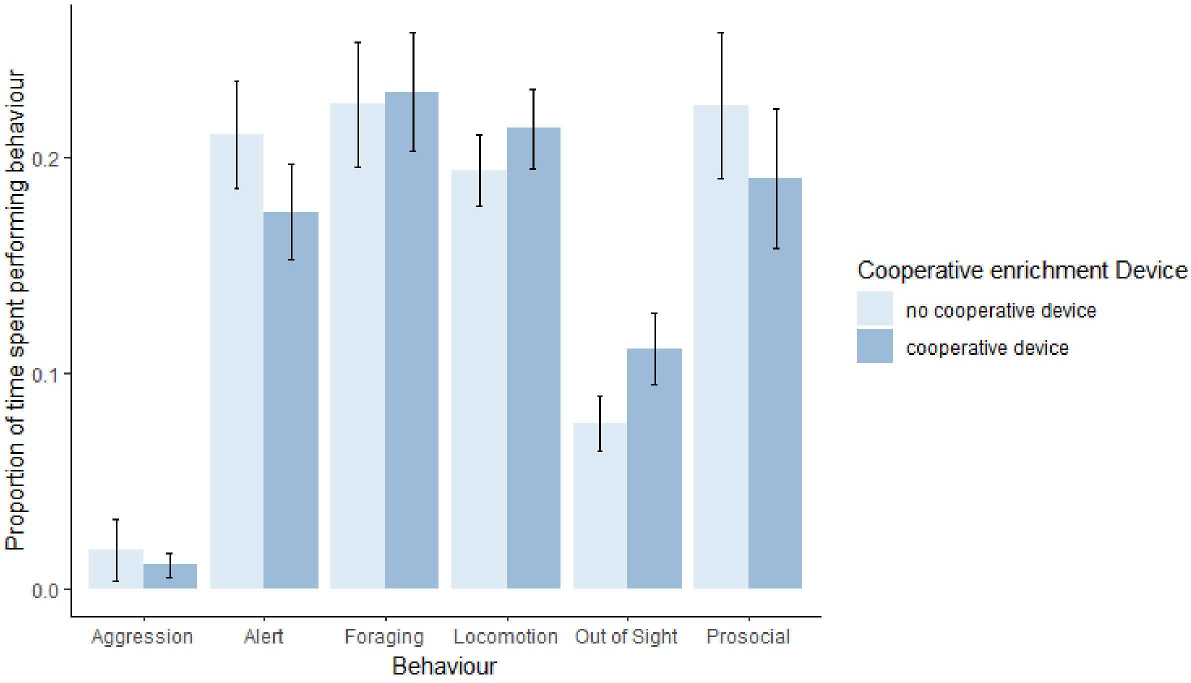

Figure 21: Proportion of time M. nigra subjects spent performing behaviours during non-presentation and presentation of the device. Error bars represent standard error.

The comparison between the full Locomotion Model and models removing the main effects or interactions revealed a significant effect of removing Macaque on overall model fit (Table 10), therefore indicating that Macaque has a significant impact on the amount of time spent locomoting. It is clear from figure 22 that there is individual variation in the time spent locomoting.

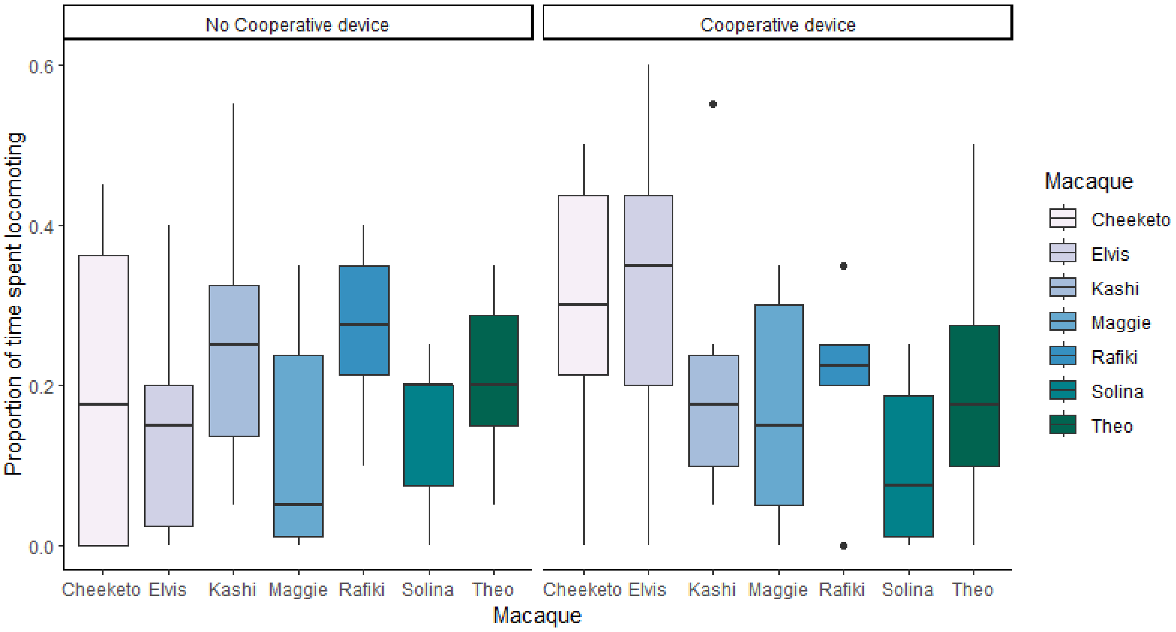

Figure 22: Proportion of time M. nigra subjects spent locomoting during non-presentation and presentation of the device

The comparison between the full Prosocial Model and models removing the main effects or interactions were all non-significant (Table 10), therefore neither of the independent variables were having a significant impact on the amount of time performing prosocial behaviour (Appendix 5).

The comparison between the full Aggression Model and models removing the main effects or interactions revealed a significant effect of removing Macaque on overall model fit (Table 10), therefore indicating that Macaque has a significant impact on the amount of time spent performing aggressive behaviour. This is due to only two individuals (Cheeketo and Elvis) performing this behaviour on rare occasions (Figure 23).

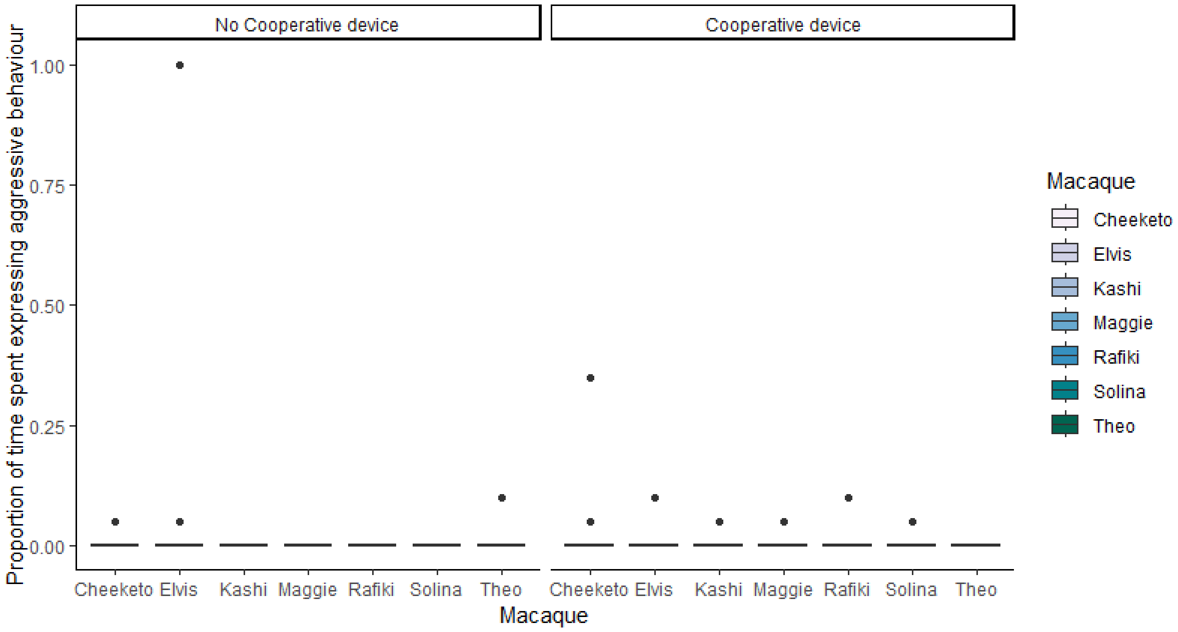

Figure 23: Proportion of time M. nigra subjects spent expressing aggressive behaviours during non-*presentation and presentation of the device.*

The comparison between the full Alert Model and models removing the main effects or interactions revealed a significant effect of removing Macaque on overall model fit (Table 10), therefore indicating that there is individual variation in the time spent performing alert behaviour (Figure 24).

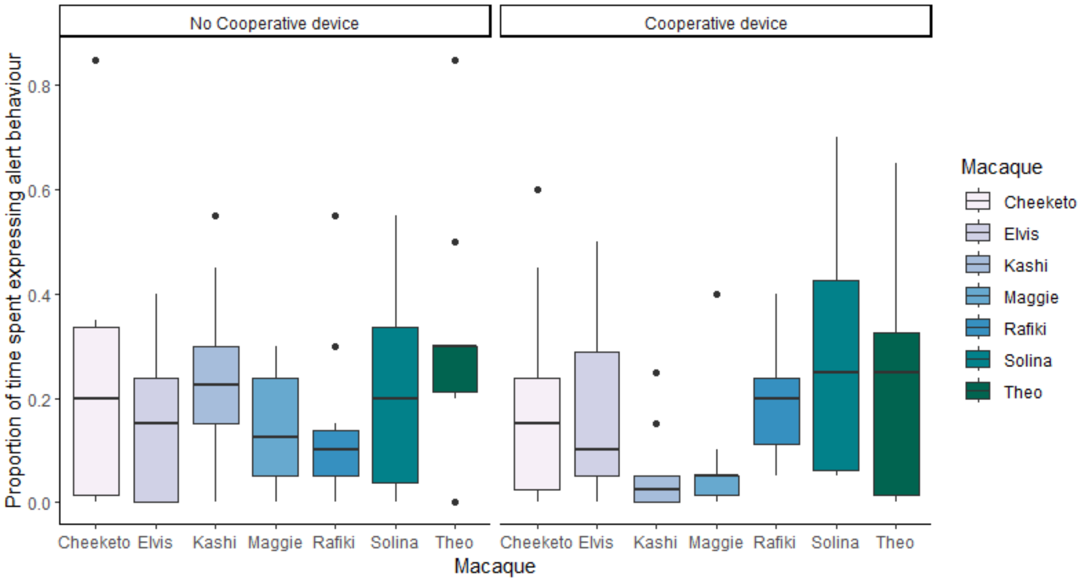

Figure 24: Proportion of time M nigra subjects spent expressing alert behaviours during non-presentation and presentation of the device.

The comparison between the full Foraging and Feeding Model and models removing the main effects or interactions were all non-significant (Table 10), therefore none of the variables were having a significant impact on the amount of time spent foraging and feeding (Appendix 5).

The comparison between the full Out of Sight Model and models removing the main effects or interactions revealed a significant effect of removing the interaction between box and macaque on overall model fit (Table 10). Whilst this needs to be interpreted with caution as there was no significant main effect of these variables, visual examination of the data does indicate that Kashi and Maggie were out of sight more often when the device was installed, whereas Rafiki and Solina were out of sight more often when the device was not installed (Figure 25).

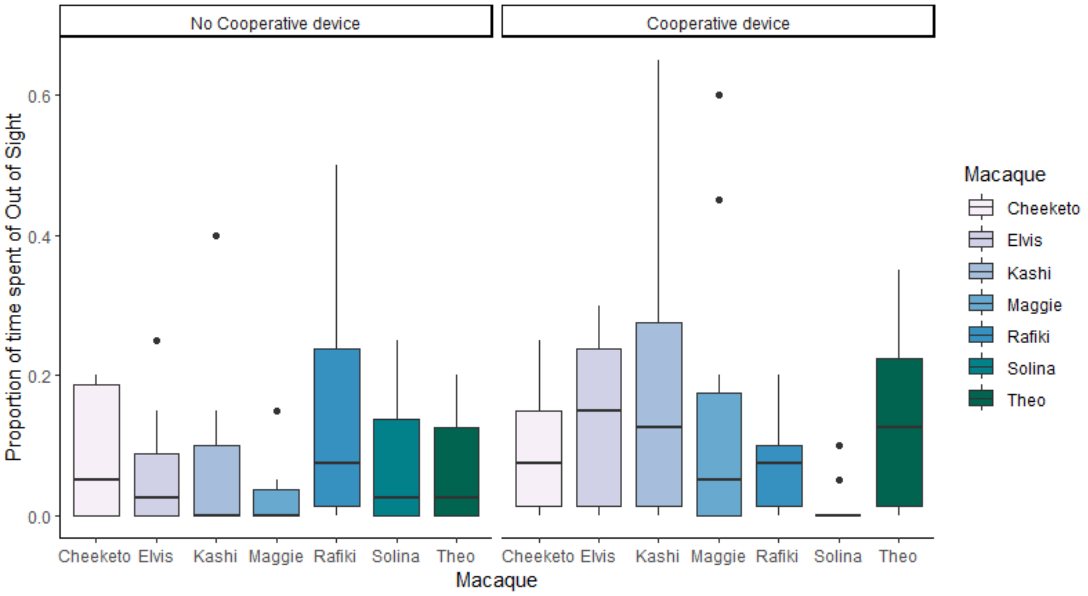

Figure 25: Proportion of time M. nigra subjects spent out of sight during non-presentation and presentation of the device.

3.2 Case study 1 – *M. nigra* video analysis

The macaque subjects did not successfully solve the cooperative task, and consequently, they did not receive any food rewards from the device across all trial instances. As a result, no data pertaining to the successful completion of the task was accessible for analysis. The examination focused on the analysis of other variables to assess the level of engagement exhibited by the macaques with the device.

3.2.1 Time interacting with the novel cooperative enrichment device

A Kruskal-Wallis test indicated a statistically significant difference in the amount of time (measured in seconds) each individual macaque spent interacting with the device, $\chi^2 = 48.243$, df = 6, $p = <0.05$. Further pairwise Wilcoxon test comparisons identified the following significant differences: Elvis spent more time interacting with the device than Cheeketo ($p = <0.01$), Kashi ($p = <0.01$) and Solina ($p = <0.05$); Cheeketo spent more time interacting with the device than Kashi ($p = <0.01$); Rafiki spent more time interacting with the device than Cheeketo ($p = <0.01$), Kashi ($p = <0.01$) and Maggie ($p = <0.01$); Solina spent more time interacting with the device than Kashi ($p = <0.01$) and Maggie ($p = <0.01$) and Theo spent more time interacting with the device than Cheeketo ($p = <0.01$), Kashi ($p = <0.01$) and Maggie ($p = <0.01$) (Figure 26).

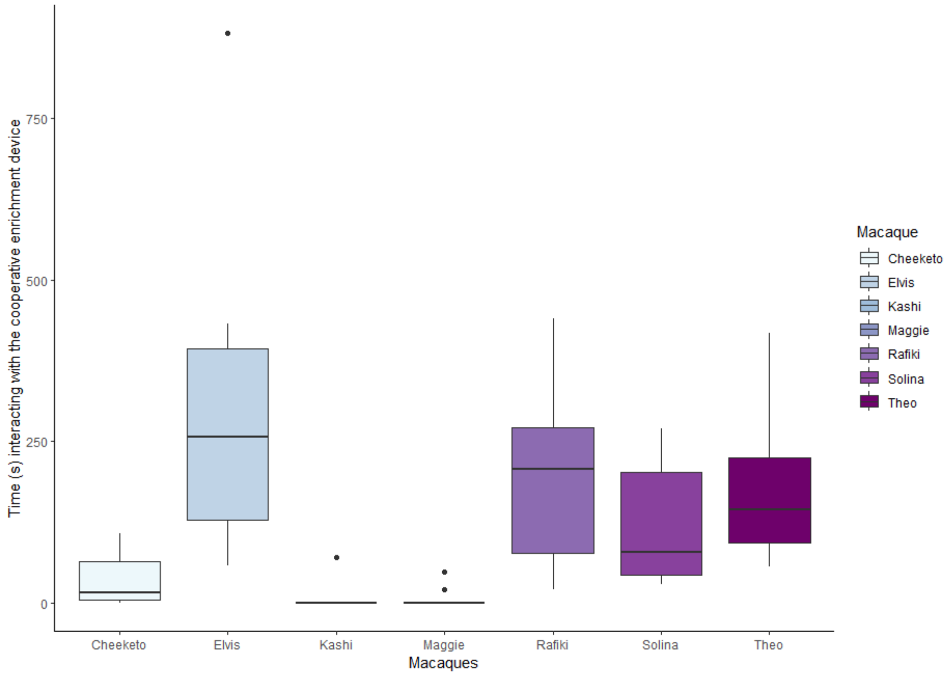

Figure 26: Boxplot of time (s) each M. nigra subject spent interacting with the device.

Kruskal-Wallis analysis indicated there was a statistically significant difference in the time spent interacting with the device between male and female subjects, with male subjects spending more time interacting with the device $\chi^2 = 9.6779$, df = 1, $p = <0.05$ (Figure 27).

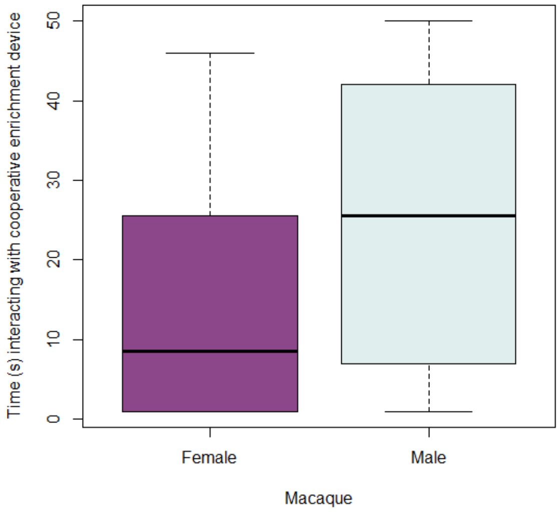

Figure 27: Boxplot of female (n=4) and male (n=3) time (s) spent interacting with the device.

Spearman's correlation determined the relationship between the number of trials and the total amount of time the subjects spent interacting with the device. There was a strong, positive linear relationship between the number of trials and the time subjects spent interacting with the device (r_s = .78, n = 10, *p* = <0.05) (Figure 28).

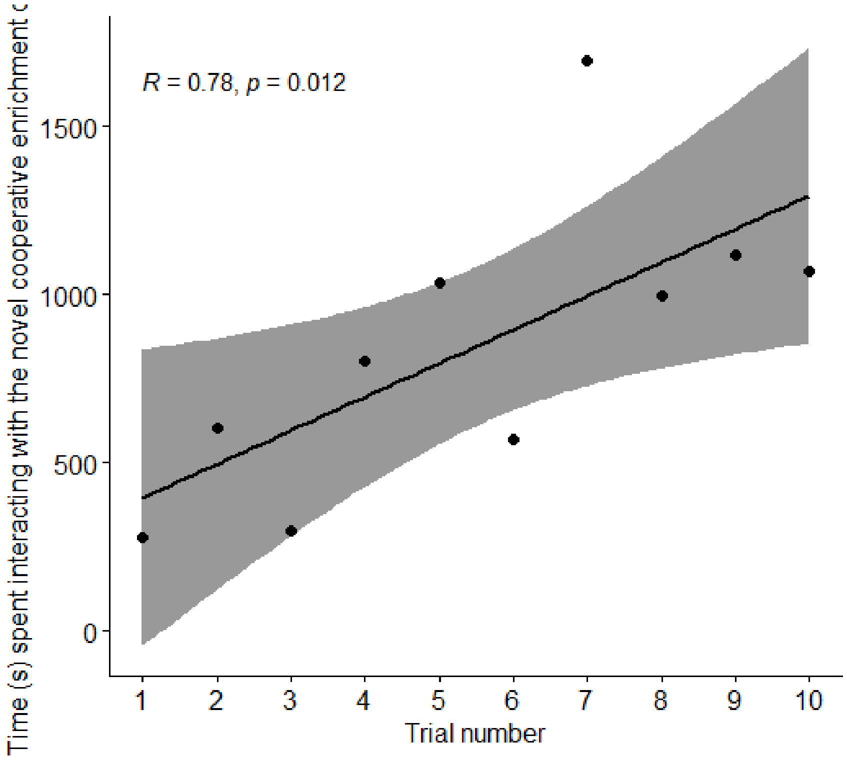

Figure 28: Spearman rank correlation - total amount of time the whole group of M. nigra spent interacting with the device over 10 trials. The shaded area represents a 95% confidence interval.

3.2.2 Aggressive acts directed at the device

A Kruskal-Wallis test indicated a statistically significant difference in the number of aggressive acts directed towards the device, $\chi^2 = 24.035$, df = 6, $p = <0.001$. Further pairwise comparisons identified the following significant differences: Cheeketo expressed more aggressive acts than Kashi ($p = <0.05$), Maggie ($p = <0.05$) and Theo ($p = <0.05$); Elvis expressed more aggressive acts than Kashi ($p = <0.05$), Maggie ($p = <0.05$) and Theo ($p = <0.05$) (Figure 29).

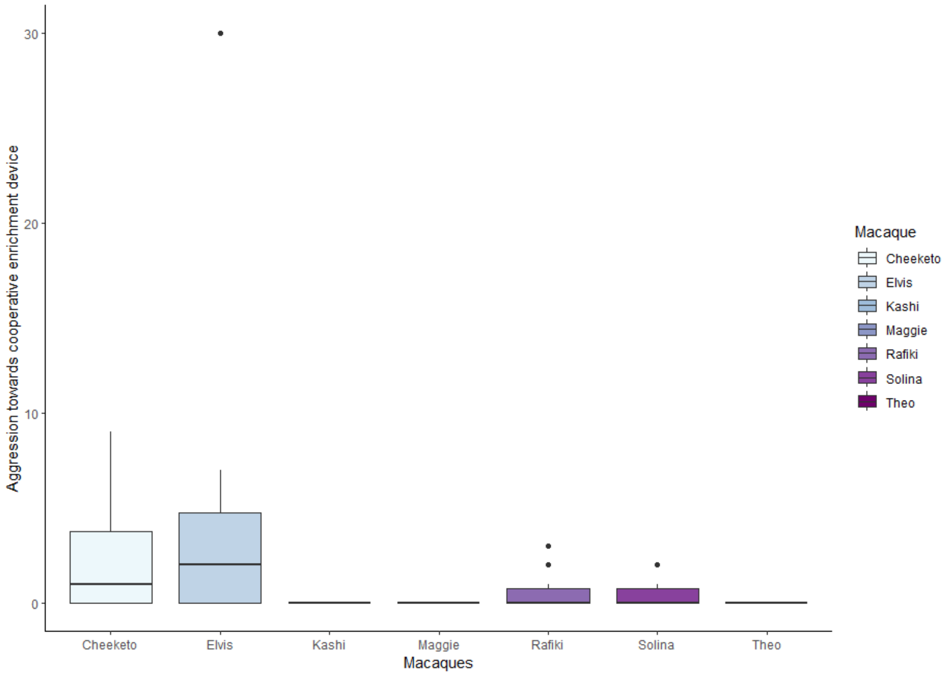

Figure 29: Number of aggressive acts directed towards the device for each M. nigra subject.

Kruskal-Wallis analysis indicated a statistically significant difference between male and female subjects, with male subjects expressing a higher number of aggressive acts towards the device $\chi^2 = 17.293$, df = 1, $p = <0.001$ (Figure 30).

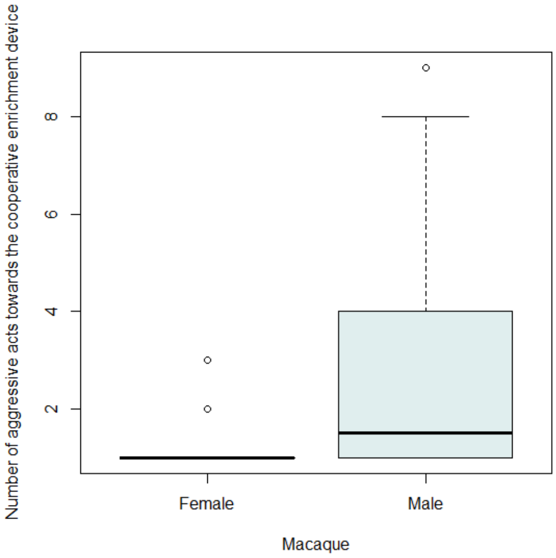

Figure 30: Boxplot of female (n=4) and male (n=3) aggressive acts towards the device.

Spearman's correlation determined the relationship between the number of trials and the number of aggressive acts directed at the device. There was no linear relationship between the number of trials and the number of aggressive acts ($r_s = .16$, n = 10, p = 0.66) (Figure 31).

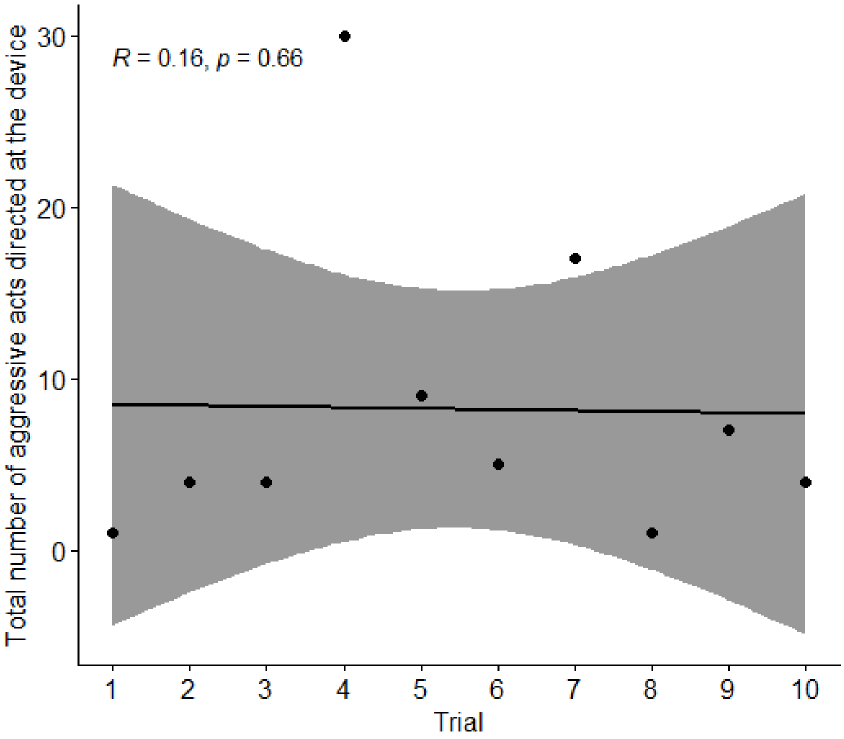

Figure 31: Spearman rank correlation - total number of aggressive acts directed at the device over the ten trials. The shaded area represents a 95% confidence interval.

3.2.3 Approaches to the device

A Kruskal-Wallis test indicated a statistically significant difference in the number of times individual subjects approached the device, $\chi^2 = 45.076$, df = 6, $p = <0.001$. Further pairwise comparisons identified the following significant differences: Elvis approached the device more often that Cheeketo ($p = <0.05$), Kashi ($p = <0.001$), Maggie ($p = <0.001$) and Solina ($p = <0.05$); Rafiki approached the device more often that Cheeketo ($p = <0.05$), Kashi ($p = <0.001$), Maggie ($p = <0.001$) and Solina ($p = <0.05$); Solina approached the device more often than Kashi ($p = <0.001$) and Maggie ($p = <0.05$); Theo approached the device more often than Cheeketo ($p = <0.05$), Kashi ($p = <0.001$), Maggie ($p = <0.001$) and Solina ($p = <0.05$) (Figure 32).

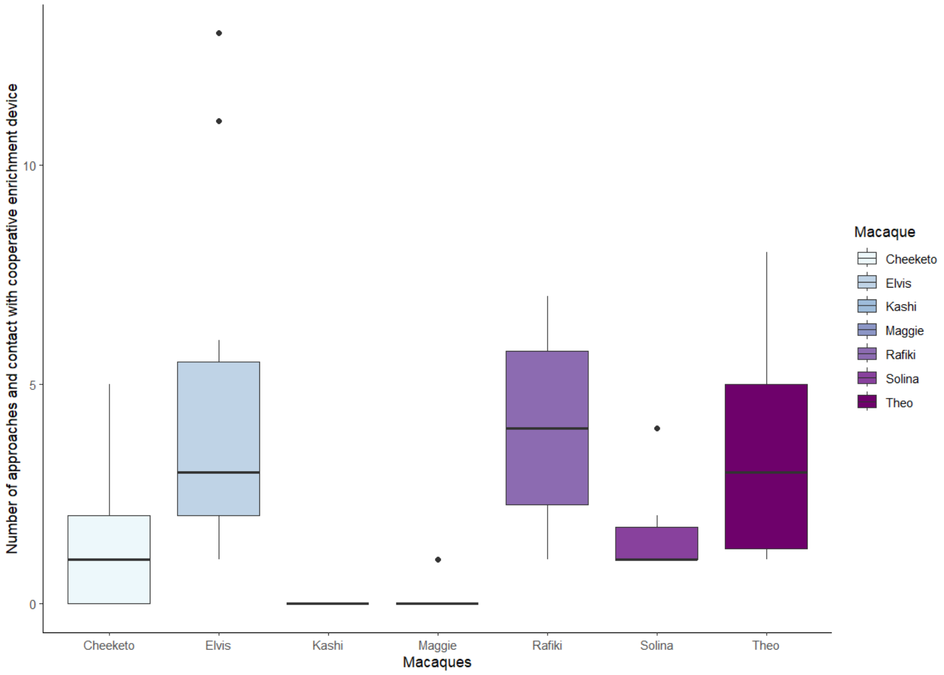

Figure 32: Boxplot of approaches to the device for M. nigra subjects.

Kruskal-Wallis analysis indicated a statistically significant difference between male and female subjects, and the number of times they approached the device, males approached the device more often $\chi^2 = 12.758$, df = 1, $p = <0.001$ (Figure 33).

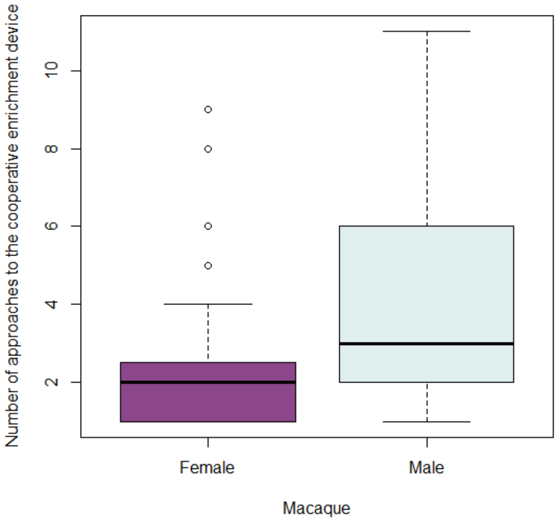

Figure 33: Number of approaches to the device between female (n=4) and male (n=3) subjects.

Spearman's correlation determined the relationship between the number of trials and the total amount of times the subjects approached the device. There was a very strong, positive linear relationship between the number of trials and the number of approaches ($r_s = .88$, n = 10, $p = <0.001$) (Figure 34).

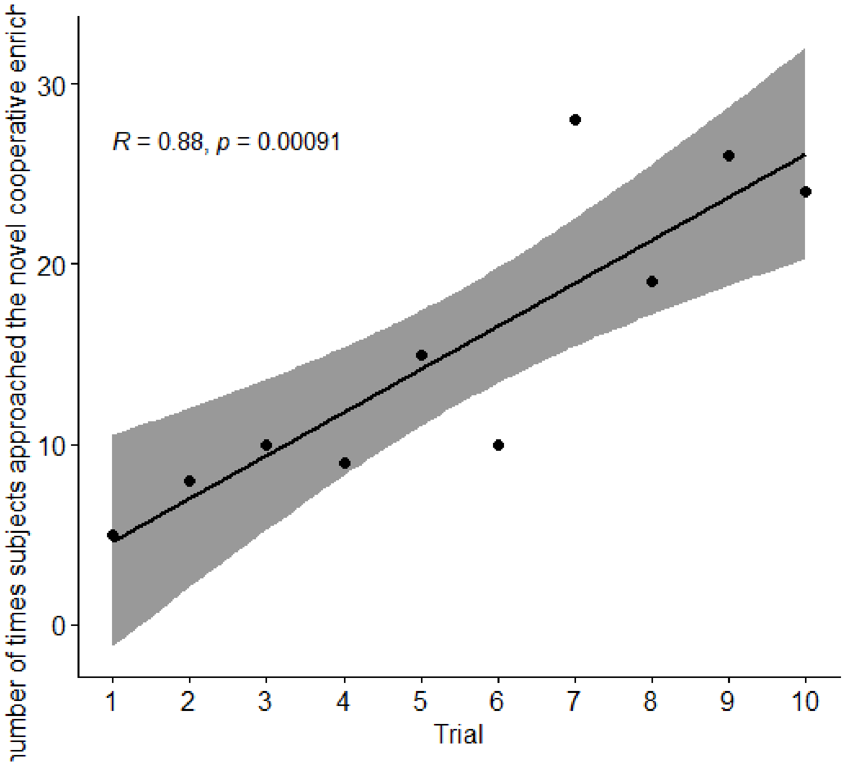

Figure 34: Spearman rank correlation - number of times subjects approached the device over the ten trials. The shaded area represents a 95% confidence interval.

3.2.4 Rope-pulls

A Kruskal-Wallis test indicated a statistically significant difference in the number of rope-pulls observed $\chi^2 = 31.115$, df = 6, $p = <0.001$. Further pairwise comparisons identified the following significant differences: Elvis had a higher number of rope-pulls than Cheeketo ($p = <0.05$) and Maggie ($p = <0.05$); Rafiki had a higher number of rope-pulls than Cheeketo ($p = <0.05$), Maggie ($p = <0.05$), Kashi ($p = <0.05$) and Solina ($p = <0.05$) (Figure 35).

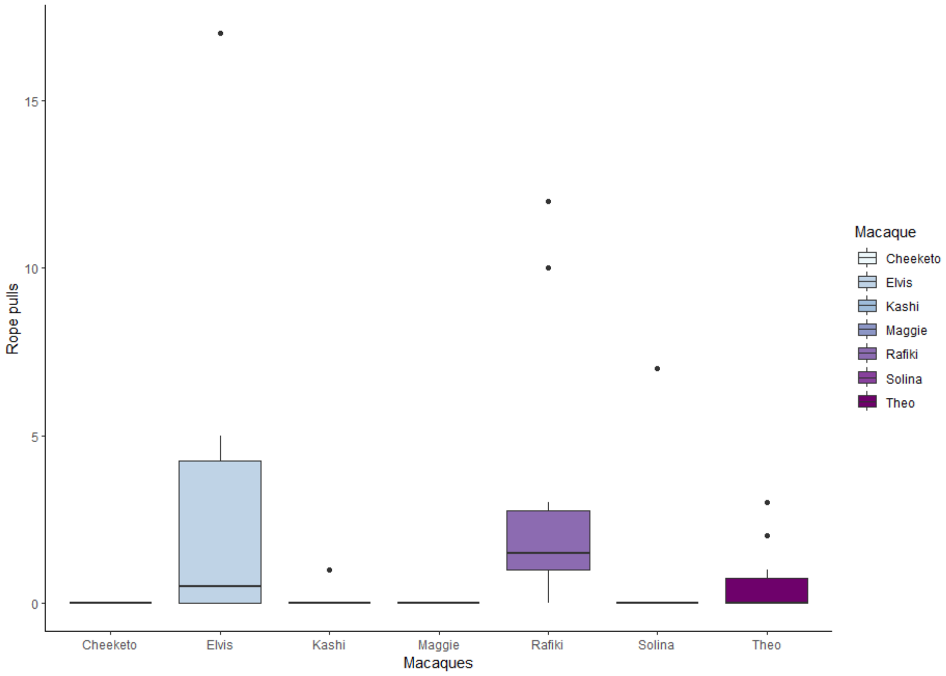

Figure 35: Number of rope-pulls made by M. nigra subjects.

Kruskal-Wallis analysis indicated that male subjects pulled the device ropes significantly more times than female subjects $\chi^2 = 10.05$, df = 1, $p = 0.001$ (Figure 36).

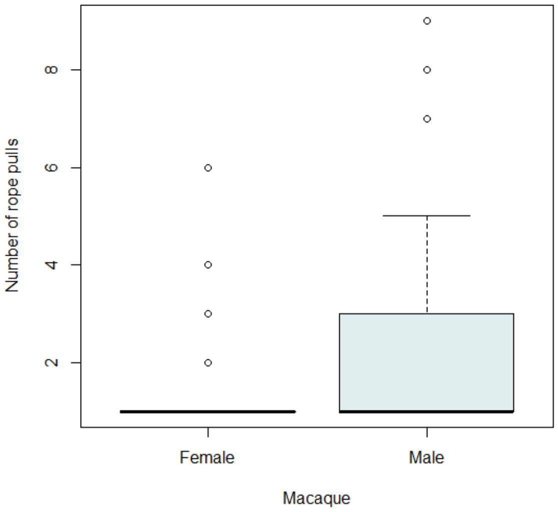

Figure 36: Boxplot of female (n=4) and male (n=3) rope-pulls.

Spearman's correlation determined the relationship between the number of trials and the total number of rope-pulls. There was a strong, positive linear relationship between the number of trials and the number of rope-pulls (r_s = .66, n = 10, *p* = <0.05) (Figure 37).

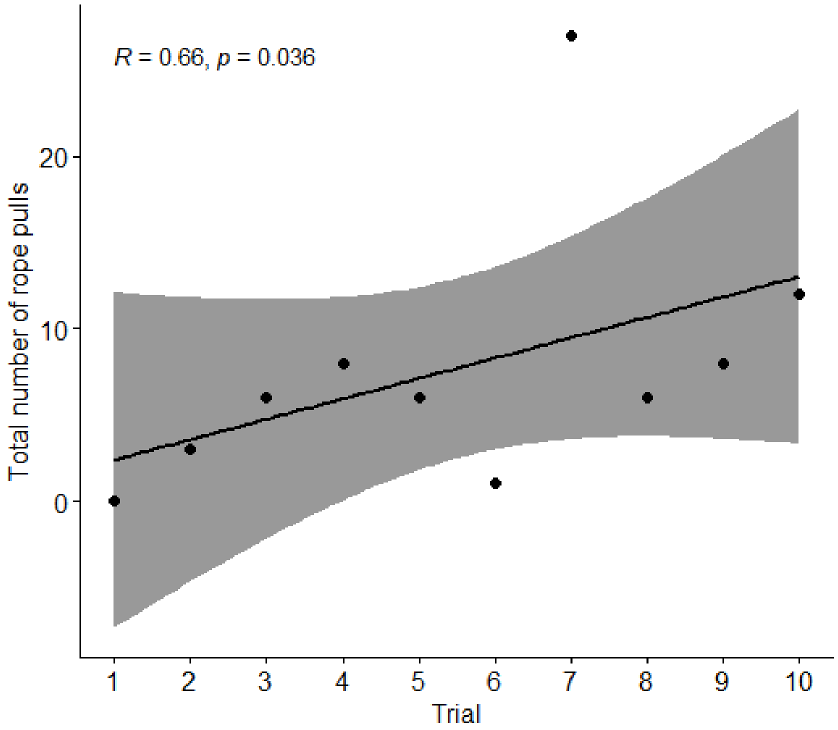

Figure 37: Spearman rank correlation - number of rope-pulls over the ten trials. The shaded area represents a 95% confidence interval.

Chi squared analysis indicated a significant difference in the number of rope-pulls associated with whether subjects were alone or socially interacting at the device χ^2 = 12.597, df = 4, *p* = <0.05 (Figure 38).

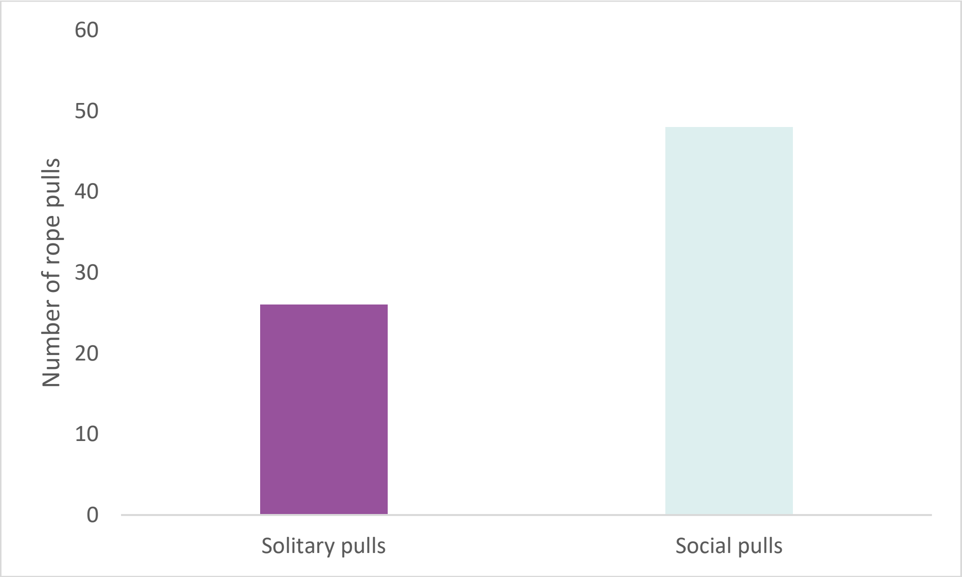

Figure 38: Number of solitary and social rope-pulls at the device.

3.2.5 Latency

A Kruskal-Wallis test indicated a statistically significant difference in latency of individual subjects to approach the device $\chi^2 = 39.458$, df = 6, *p* = <0.001. Further pairwise comparisons identified a significant difference between: Kashi had a significantly higher latency to approach the device than Cheeketo (*p* = <0.05), Elvis (*p* = <0.001), Rafiki (*p* = <0.001), Solina (*p* = <0.001) and Theo (*p* = <0.001); Maggie had a significantly higher latency to approach the device than Cheeketo (*p* = <0.05), Elvis (*p* = <0.001), Rafiki (*p* = <0.05), Solina (*p* = <0.05), and Theo (*p* = <0.05) (Figure 39).

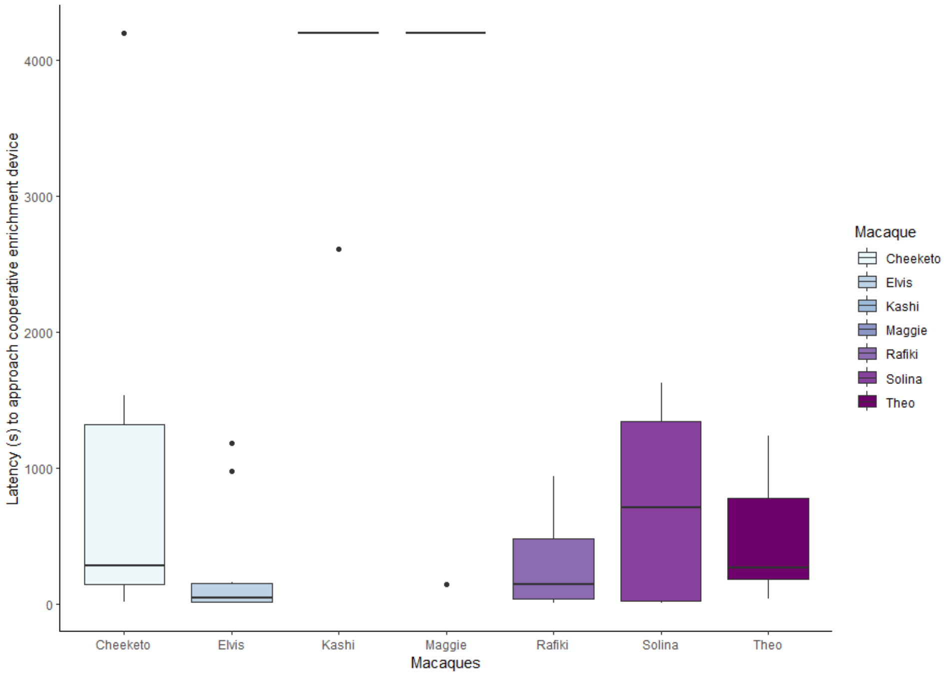

Figure 39: Latency (s) to approach the device for individual M. nigra subjects.

Kruskal-Wallis analysis indicated there was a statistically significant difference, males showed significantly shorter latency to approach the device $\chi^2 = 16.329$, df = 1, *p* = <0.001 (Figure 40), females may have been slower to approach, because of males dominating the device.

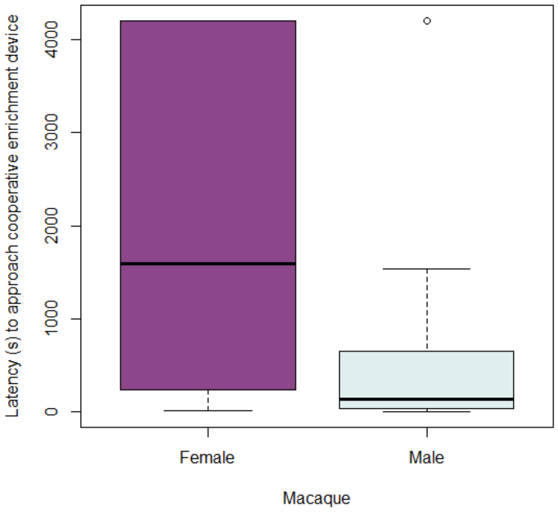

Figure 40: Latency (s) of female (n=3) and male (n=3) M. nigra to approach the device.

Spearman's correlation determined the relationship between the number of trials and latency (s) to approach the device. There was a weak negative relationship between the number of trials and latency (r_s = .22, n = 10, *p* = 0.54) (Figure 41).

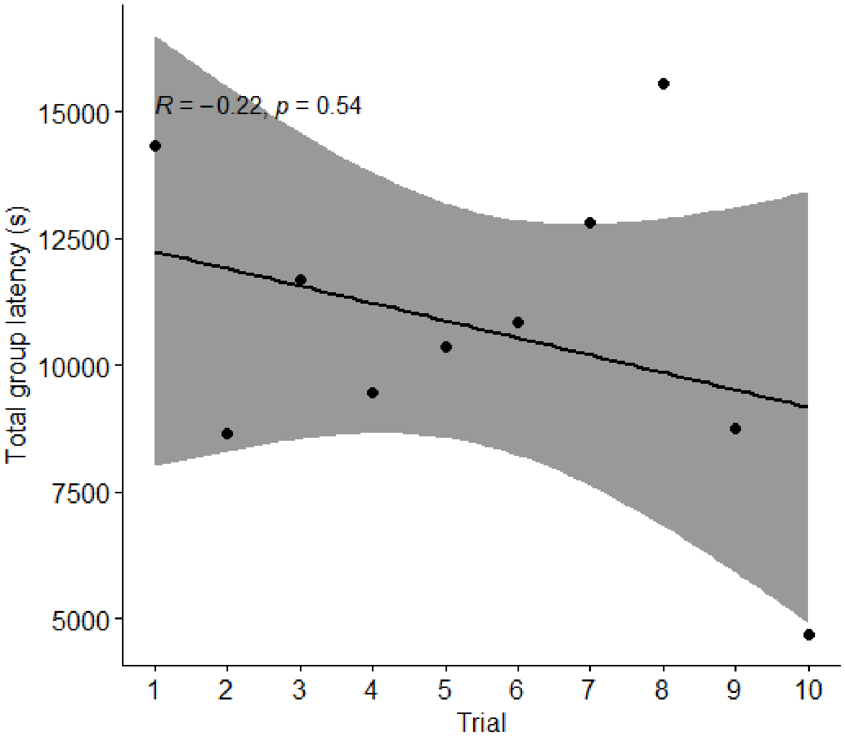

Figure 41: Spearman rank correlation - Latency (s) of subjects to approach the device over ten trials. The shaded area represents a 95% confidence interval.

3.2.6 Social vs solitary rope-pulls

Ropes pulls for the group were analysed, two subjects were removed from the analysis: Cheeketo due to the lack of rope-pulls and Maggie due to no approach or interaction with the device. For the remaining five subjects, there was a significant difference in the number of rope-pulls when individuals were socially interacting at the device $\chi^2 = 12.597$, df = 4, $p = <0.05$, this difference appears to be driven by Solina and Rafiki (Figure 42).

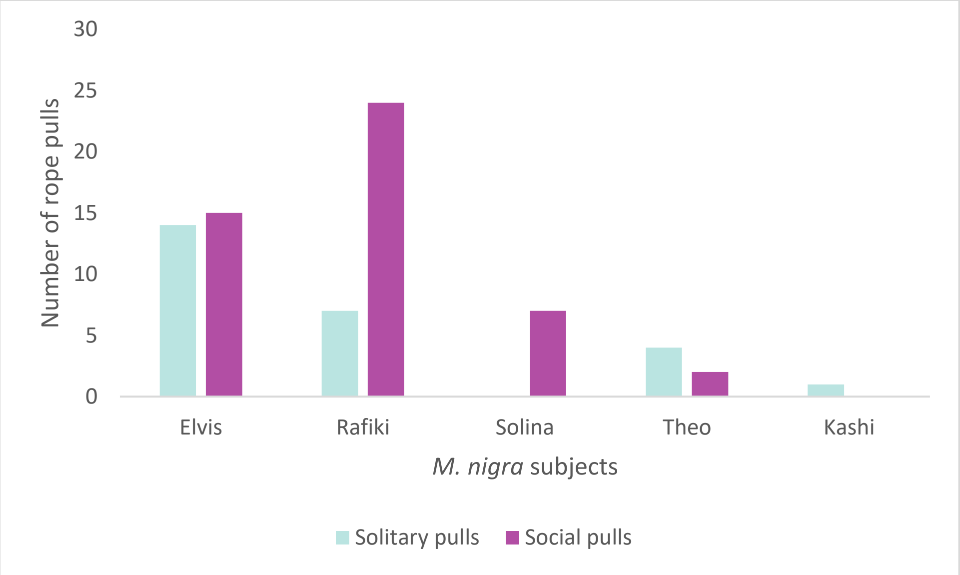

Figure 42: Number of solitary vs social rope-pulls of individual subjects.

3.2.7 Social interactions

Table 11: M. nigra subjects dyad interaction matrix, recorded social interactions at the device (column = initiator (first individual to approach the device, row = joiner (individual who joined initiator at the device).

	Cheeketo	Elvis	Rafiki	Solina	Maggie	Theo	Kashi
Cheeketo		1	0	0	0	0	0
Elvis	6		10	4	1	5	0
Rafiki	1	6		2	1	2	0
Solina	2	1	2		0	0	1
Maggie	0	0	0	0		0	0
Theo	2	2	7	3	0		0
Kashi	0	0	0	0	0	0	

Data was used to plot an iGephi matrix of subject interactions, and shows that Rafiki, Theo, Cheeketo and Solina directed social interactions with Elvis (Figure 43). Kashi was only recorded interacting once, as a joiner with Solina. Rafiki interacted more often with Elvis and Theo than other individuals. Cheeketo was only recorded as an initiator once.

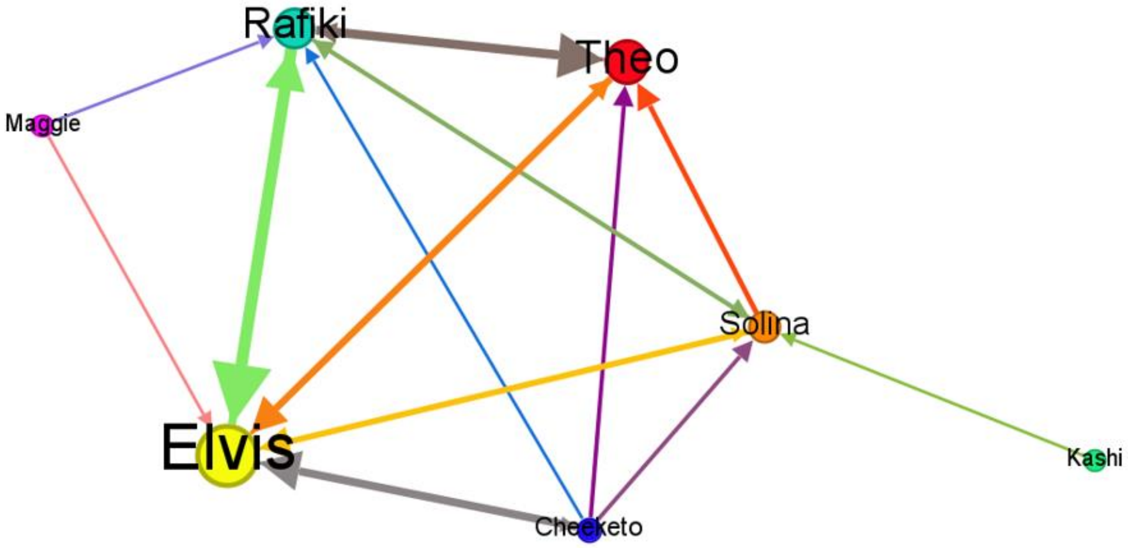

Figure 43: Interaction matrix of M. nigra subjects at the device, arrows indicate the direction of interaction, the larger the arrow head, the more interactions in that direction. The width of the interaction lines indicates frequency of interactions, the wider the line the more interactions.

3.2.8 Levels of relatedness

Levels of relatedness for the subjects were calculated using approximate relatedness coefficients (Table 12).

Table 12: Relatedness coefficients (r) for M. nigra subjects

Subject	Subject	Relatedness Coefficient (r)
Cheeketo	Elvis	0.5
Cheeketo	Rafiki	0.5
Cheeketo	Solina	0
Cheeketo	Maggie	0
Cheeketo	Theo	0
Cheeketo	Kashi	0.5
Elvis	Rafiki	0.25
Elvis	Solina	0.5
Elvis	Maggie	0.25
Elvis	Theo	0.125
Elvis	Kashi	0.5
Rafiki	Solina	0.125
Rafiki	Maggie	0.25
Rafiki	Theo	0.5
Rafiki	Kashi	0.25
Solina	Maggie	0.5
Solina	Theo	0.25
Solina	Kashi	0.5
Maggie	Theo	0.5
Maggie	Kashi	0.25
Theo	Kashi	0.125

Chi squared analysis indicated a significant difference in the frequency of interactions with the device associated with levels of relatedness $\chi^2 = 16.051$, df = 3, $p = <0.05$, there were significantly less interactions with the device between unrelated individuals (Figure 44).

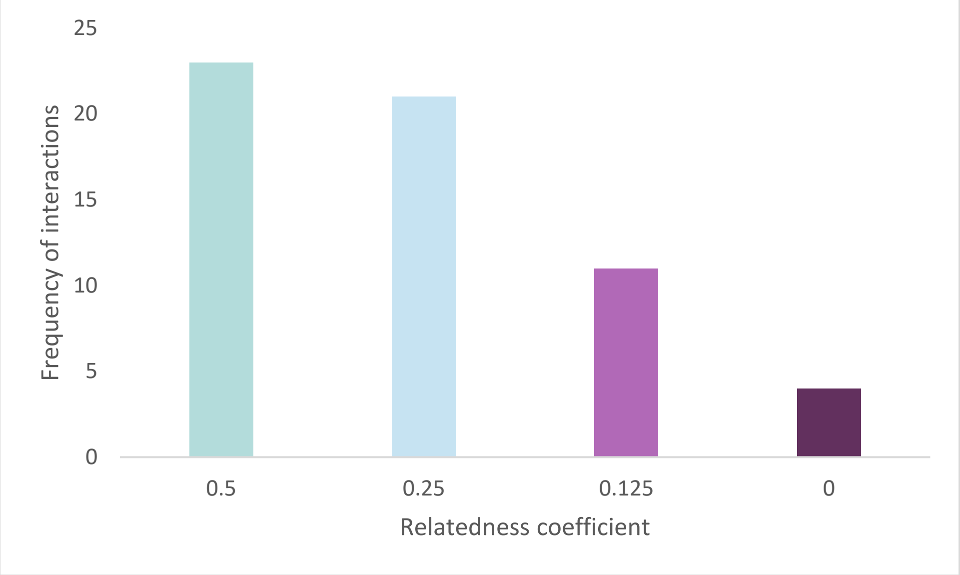

Figure 44: Frequency of interactions associated with relatedness coefficients.

3.3 Case study 2 – *C. capucinus* activity budget

Drop 1 Chi Squared examined the significance of removing each main effect or interaction from the original model. These results are reported in Table 13.

In the overall quasibinomial GLM models, there was no significant effect of the condition: no cooperative enrichment device vs. cooperative enrichment device, on the proportion of time subjects spent performing behaviours (Table 13 and Figure 45).

Table 13: Quasibinomial GLM models, including model refinement

Behaviour	Independent variables	Deviance	Drop 1 Chi Squared p value
Locomotion	Box	42.40	0.65
	Capuchin	48.71	<0.05
	Box : Capuchin	42.24	<0.05
Foraging and feeding	Box	95.73	0.34
	Capuchin	97.98	0.36
	Box : Capuchin	94.72	<0.05
Prosocial	Box	96.01	0.81
	Capuchin	96.65	0.88
	Box : Capuchin	96.95	0.72
Solitary	Box	81.43	0.28
	Capuchin	82.22	0.59
	Box : Capuchin	80.17	0.72
Interacting with environmental enrichment	Box	114.16	0.66
	Capuchin	121.08	0.08
	Box : Capuchin	113.96	0.83
Aggression	Box	0.48	<0.01
	Capuchin	0.62	<0.01
	Box : Capuchin	0.35	1
Out of sight	Box	3.89	0.86
	Capuchin	4.01	0.79
	Box : Capuchin	3.89	0.54

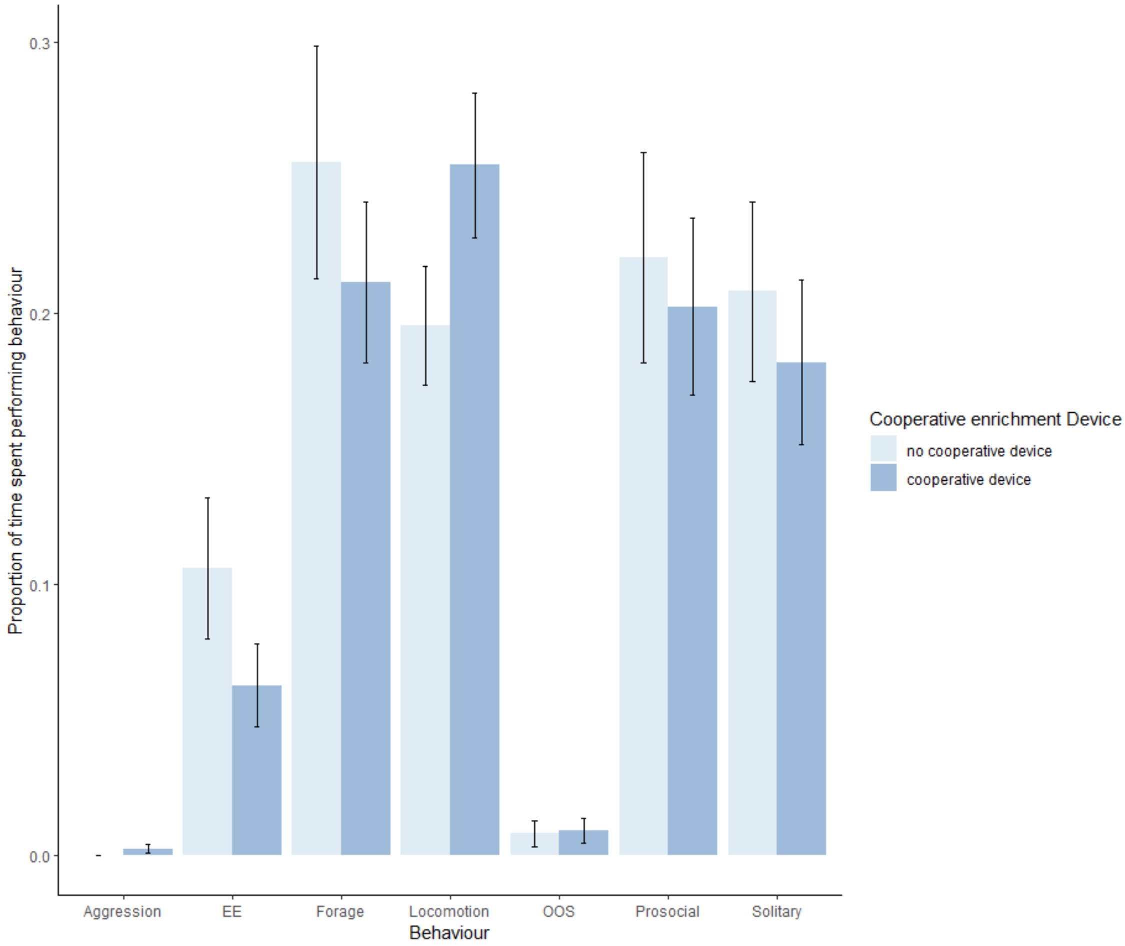

Figure 45: An overview of the proportion of time C. capucinus spent performing behaviours during non-presentation and presentation of the device. Error bars represent standard error.

The comparison between the full Locomotion Model and models removing the main effects or interactions revealed a significant effect of removing the interaction between box and capuchin and capuchin on overall model fit (Table 13 and Figure 46).

Locomotion increased for all individuals during the presentation of the cooperative enrichment device. This increase was affected by individual, figure 45 illustrates that whilst all individuals increased locomotion, this increase was greater in certain individuals.

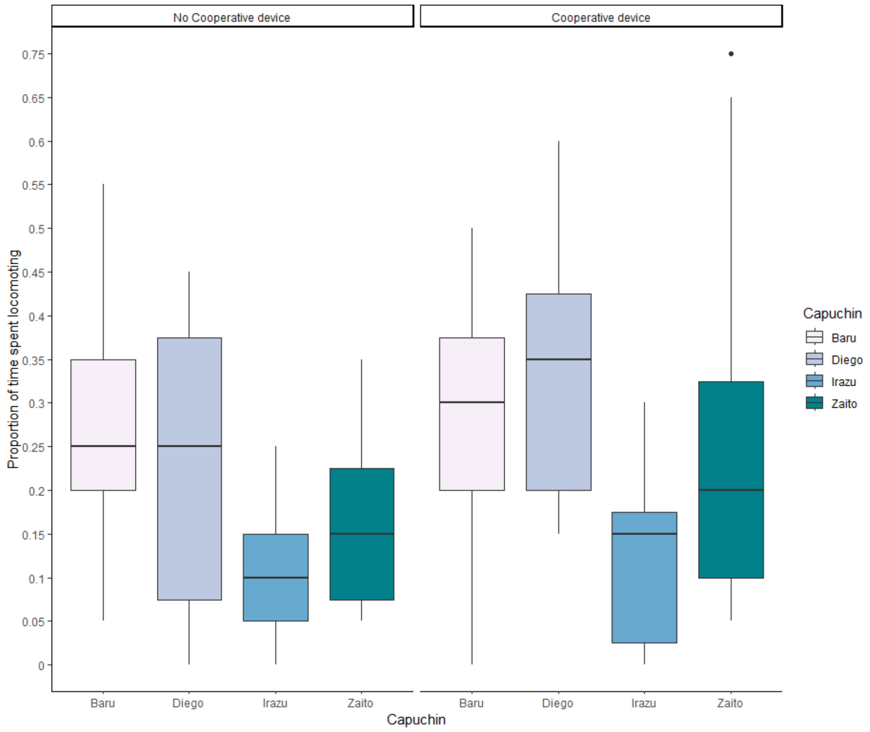

Figure 46: Proportion of time C. capucinus subjects spent locomoting during non-presentation and presentation of the device.

The comparison between the full Foraging and Feeding Model and models removing the main effects or interactions revealed a significant effect of removing the interaction between box and Capuchin on overall model fit (Table 13 and Figure 47). This needs to be interpreted with caution as there is no significant main effect of these variables.

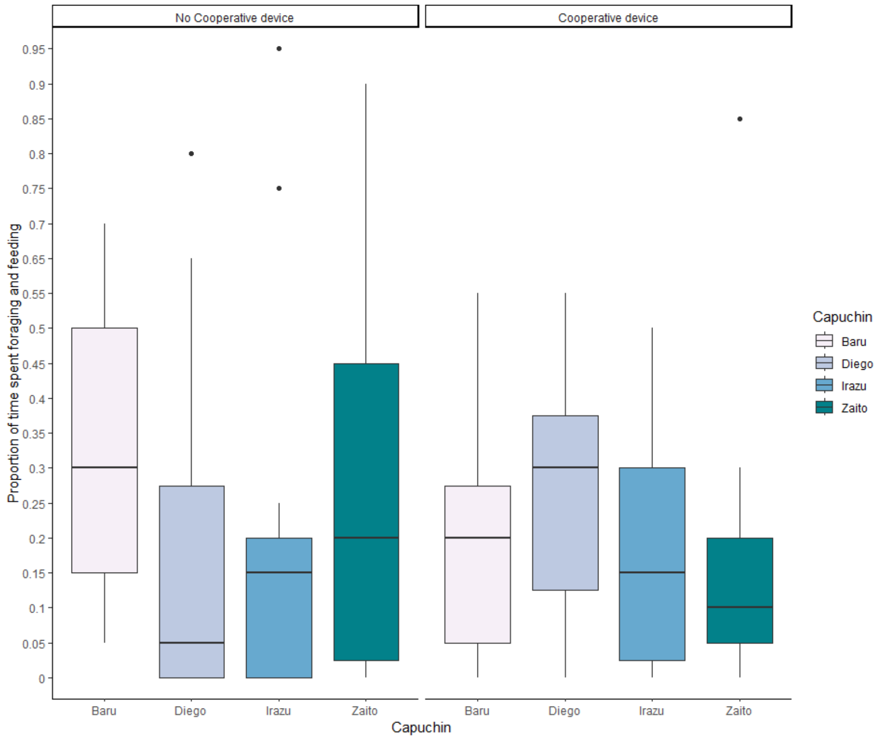

Figure 47: Proportion of time C. capucinus subjects spent foraging and feeding during non-presentation and presentation of the device.

The comparison between the full Prosocial Model and models removing the main effects or interactions were all non-significant (Table 13), therefore none of the variables were having a significant impact on the amount of time spent performing prosocial behaviour (Appendix 5).

The comparison between the full Solitary Model and models removing the main effects or interactions were all non-significant (Table 13), therefore none of the variables were having a significant impact on the amount of time spent performing solitary behaviour (Appendix 5).

The comparison between the full Environmental Enrichment Model and models removing the main effects or interactions were all non-significant (Table 13), therefore none of the variables were having a significant impact on the amount of time spent interacting with environmental enrichment (Appendix 5).

The comparison between the full Aggression Model and models removing the main effects or interactions revealed a significant effect. However, only one individual (Zaito) exhibited aggressive behaviour, this lack of data impacts on the reliability of significance identified (Table 13). Figure 48 illustrates that Zaito was only aggressive when the enrichment device was presented.

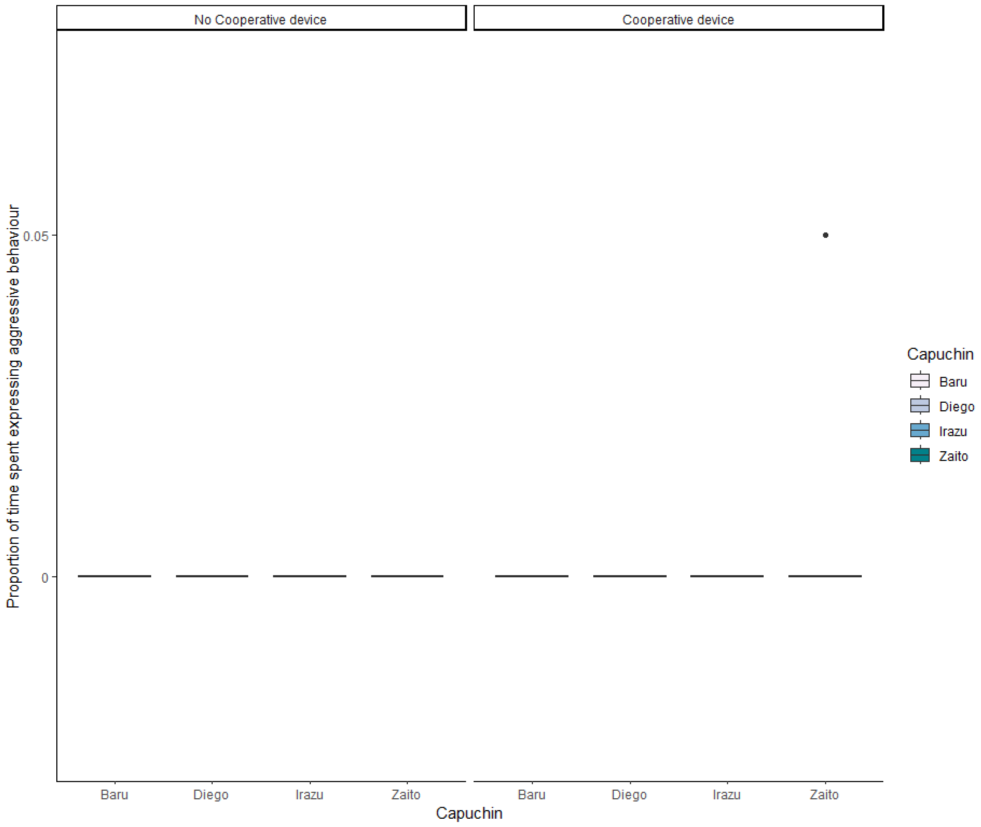

Figure 48: Proportion of time C. capucinus subjects spent expressing aggressive behaviour during no-presentation and presentation of the device.

The comparison between the full Out of Sight Model and models removing the main effects or interactions were all non-significant (Table 13), therefore none of the variables were having a significant impact on the amount of time subjects were out of sight (Appendix 5).

3.4 Case study 2 – *C. capucinus* video analysis

3.4.1 Proportion of time in proximity to the device

A Kruskal-Wallis test indicated a statistically significant difference in the proportion of time individuals spent in proximity to the device $\chi^2 = 21.693$, df = 3, *p* = <0.001. Further pairwise comparisons identified the following significant differences: Baro spent more time within proximity of the device than Zaito (*p* = <0.01); Diego spent more time within proximity of the device than Zaito (*p* = <0.01) and Irazu spent more time within proximity of the device than Zaito (*p* = <0.05) (Figure 49).

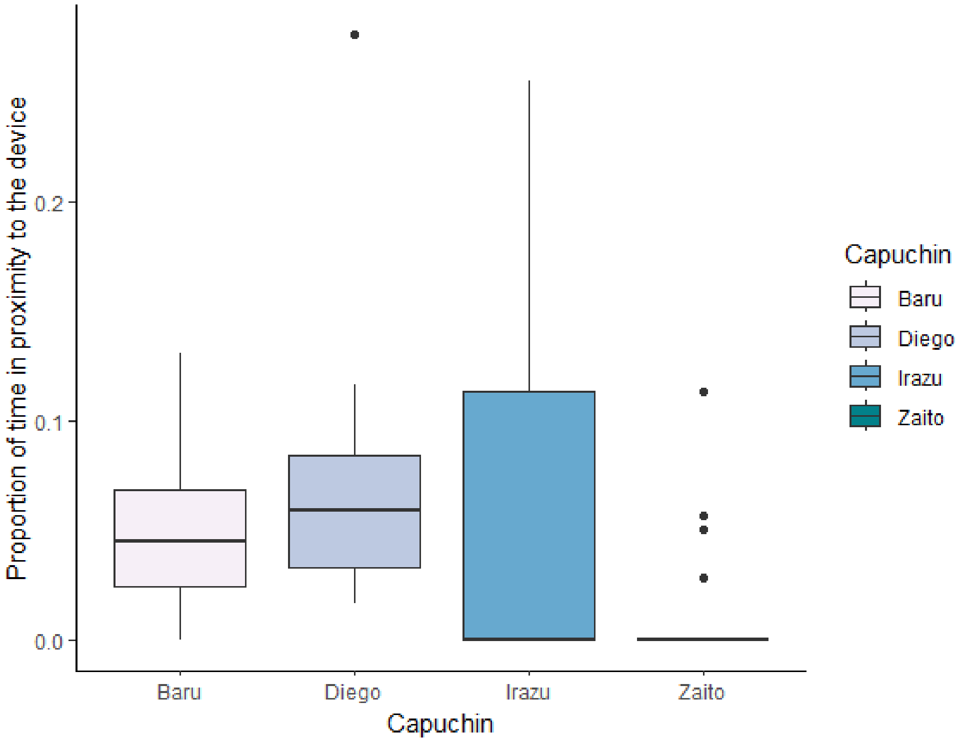

Figure 49: Proportion of time C. capucinus subjects spent in proximity to the device.

Spearman's correlation determined the relationship between the number of trials and the proportion of time subjects spent in proximity to the device. There was no linear relationship between the number of trials and the proportion of time in proximity to the device ($r_s = .15$, n = 9, *p* = 0.71) (Figure 50).

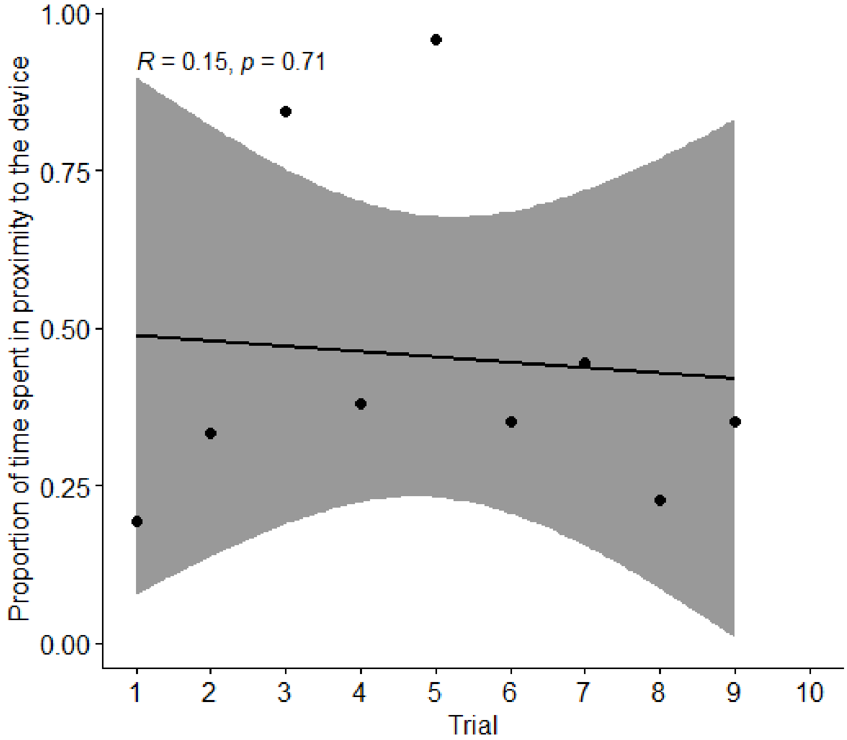

Figure 50: Spearman rank correlation - proportion of time spent in proximity to the device over the nine trials. The shaded area represents a 95% confidence interval.

3.4.2 Proportion of time interacting with the device

A Kruskal-Wallis test indicated a statistically significant difference in the proportion of time individuals spent interacting with the device $\chi^2 = 44.894$, df = 3, $p = <0.001$. Further pairwise comparisons identified the following significant differences: Irazu spent more time interacting with the device than Baru ($p = <0.01$) and Diego ($p = <0.01$); Zaito spent more time interacting with the device than Baru ($p = <0.01$) and Diego ($p = <0.01$) (Figure 51).

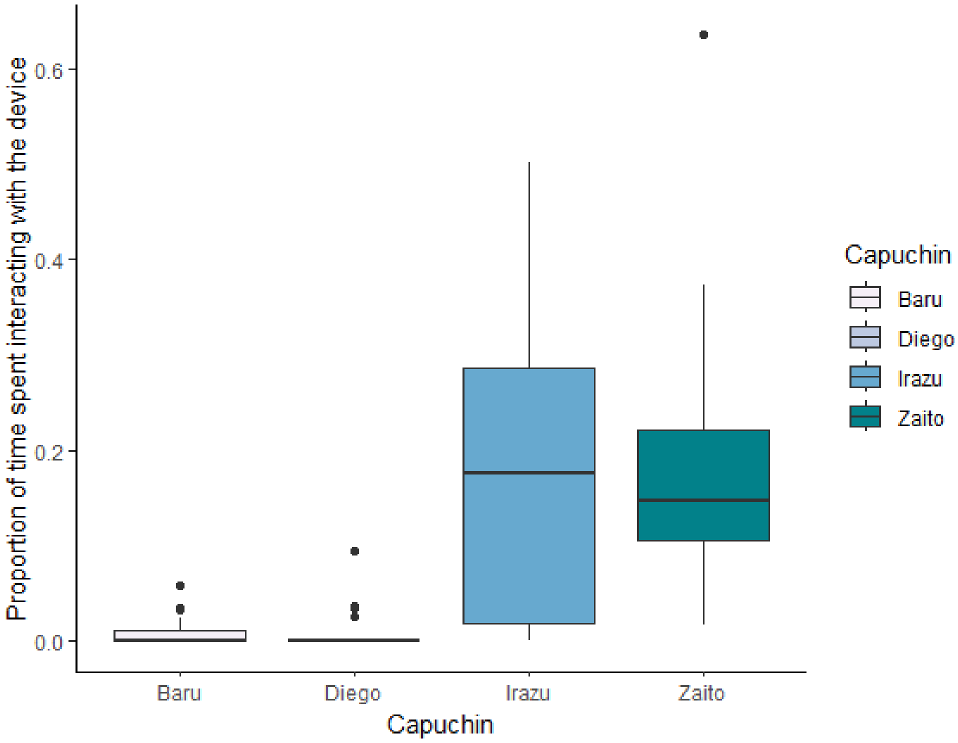

Figure 51: Proportion of time C. capucinus subjects spent interacting with the device.

Spearman's correlation determined the relationship between the number of trials and the proportion of time subjects spent interacting with the device. There was no linear relationship between the number of trials and the proportion of time spent interacting with the device ($r_s = -.01$, n = 9, $p = 0.81$) (Figure 52).

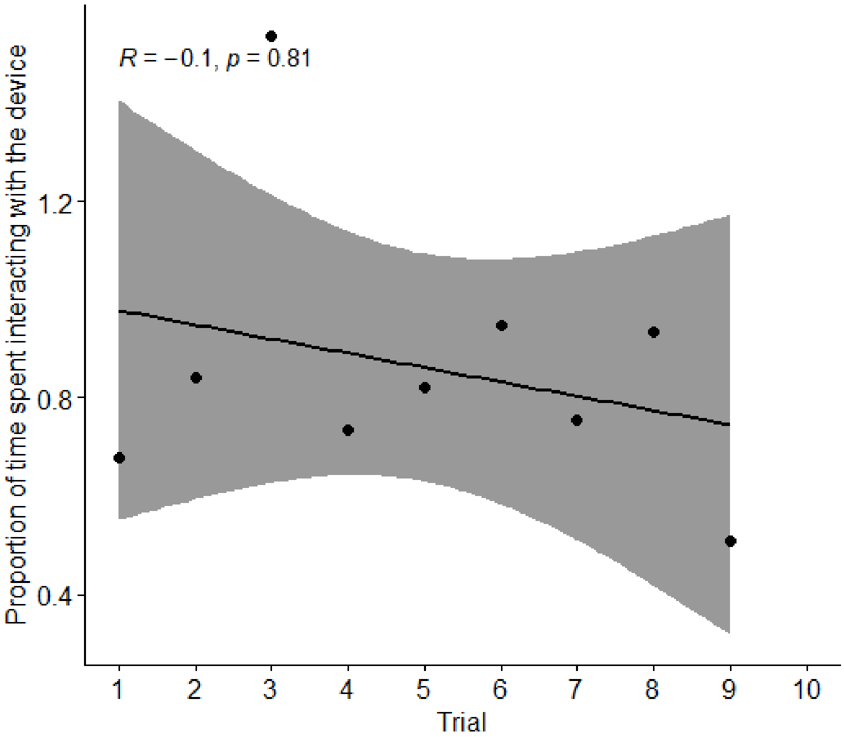

Figure 52: Spearman rank correlation - proportion of time subjects spent interacting with the device over the nine trials. The shaded area represents a 95% confidence interval.

3.4.3 Rope-pulls

A Kruskal-Wallis test indicated a statistically significant difference in the number of rope-pulls observed $\chi^2 = 26.145$, df = 3, $p = <0.001$. Further pairwise comparisons identified the following significant differences: Zaito pulled the ropes more often than Baru ($p = <0.01$), Diego ($p = <0.01$) and Irazu ($p = <0.01$) (Figure 53).

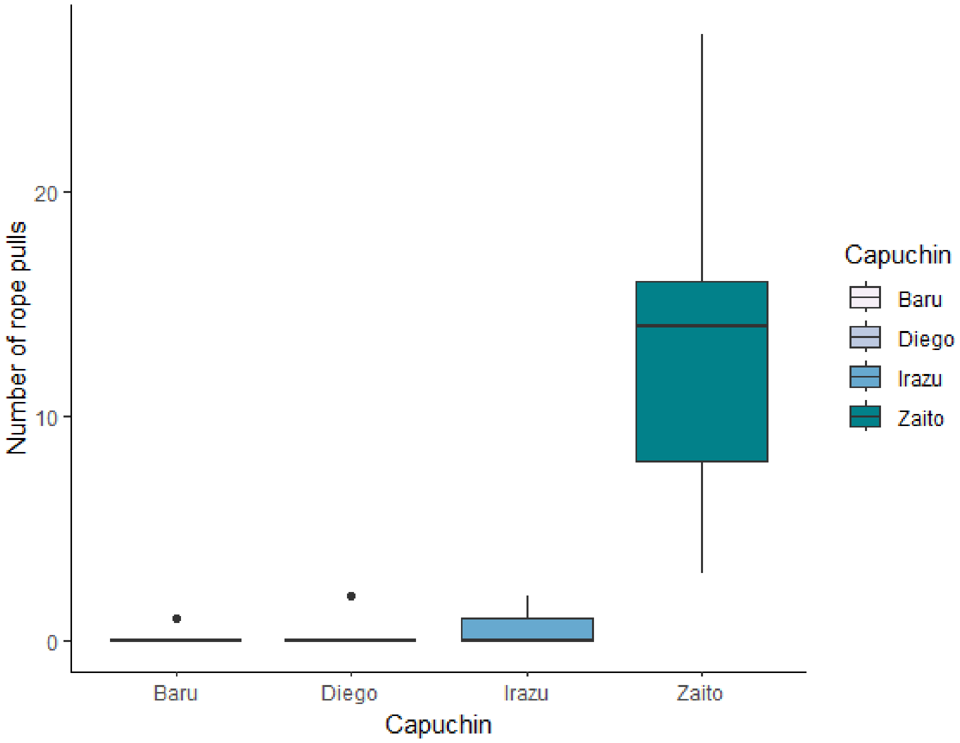

Figure 53: Number of rope-pulls made by C. capucinus subjects.

Kruskal-Wallis analysis indicated there was a statistically significant difference between adult and juvenile subjects, with adults pulling the ropes more often $\chi^2 = 12.592$, df = 1, $p = <0.001$ (Figure 54).

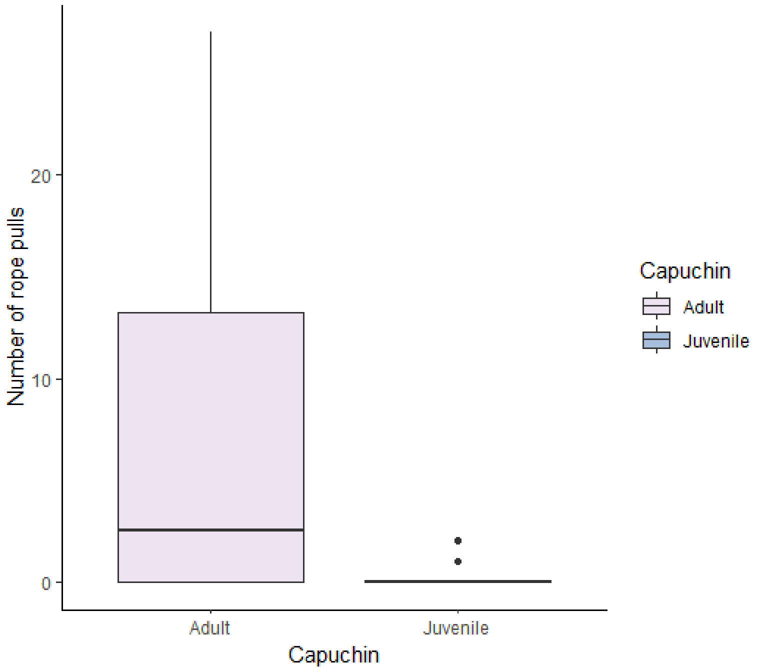

Figure 54: Boxplot of adult (n=2) and juvenile (n=2) rope-pulls.

Spearman's correlation determined the relationship between the number of trials and the number of rope-pulls. There is a moderate correlation between the number of trials and number of rope-pulls (r_s = .46, n = 9, *p* = 0.21) (Figure 55).

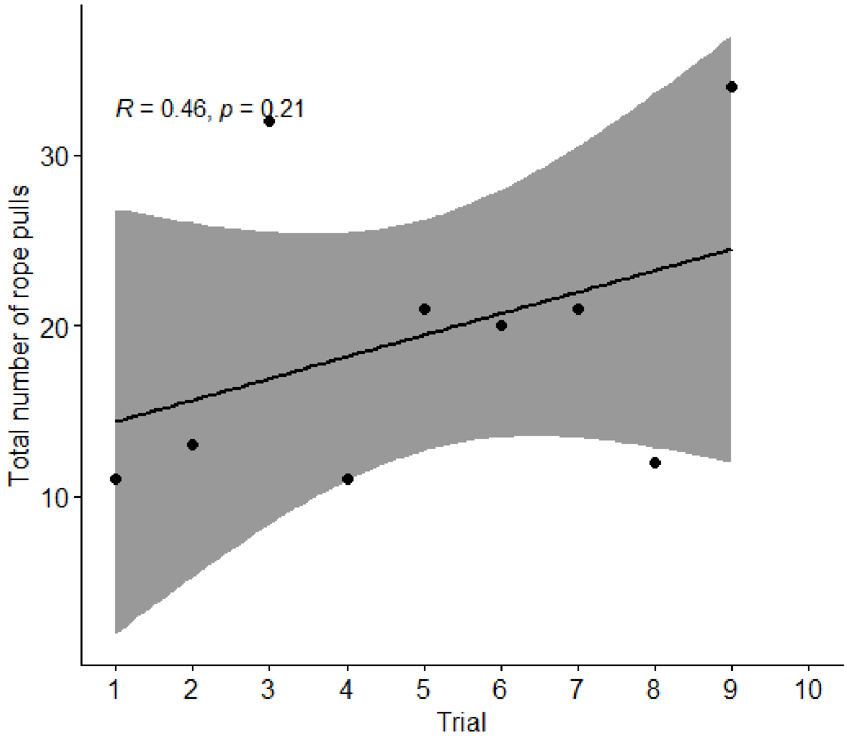

Figure 55: Spearman rank correlation - total number of rope-pulls over the nine trials. The shaded area represents a 95% confidence interval.

3.4.4 Access to food

A Kruskal-Wallis test indicated a statistically significant difference in the number of times individuals accessed food from the device $\chi^2 = 27.213$, df = 3, *p* = <0.001. Further pairwise comparisons identified the following significant difference: Irazu accessed food from the device more often than Baru (*p* = <0.01) and Diego (*p* = <0.01); Zaito accessed food from the device more often than Baru (*p* = <0.01), Diego (*p* = <0.01) and Irazu (*p* = <0.01) (Figure 56).

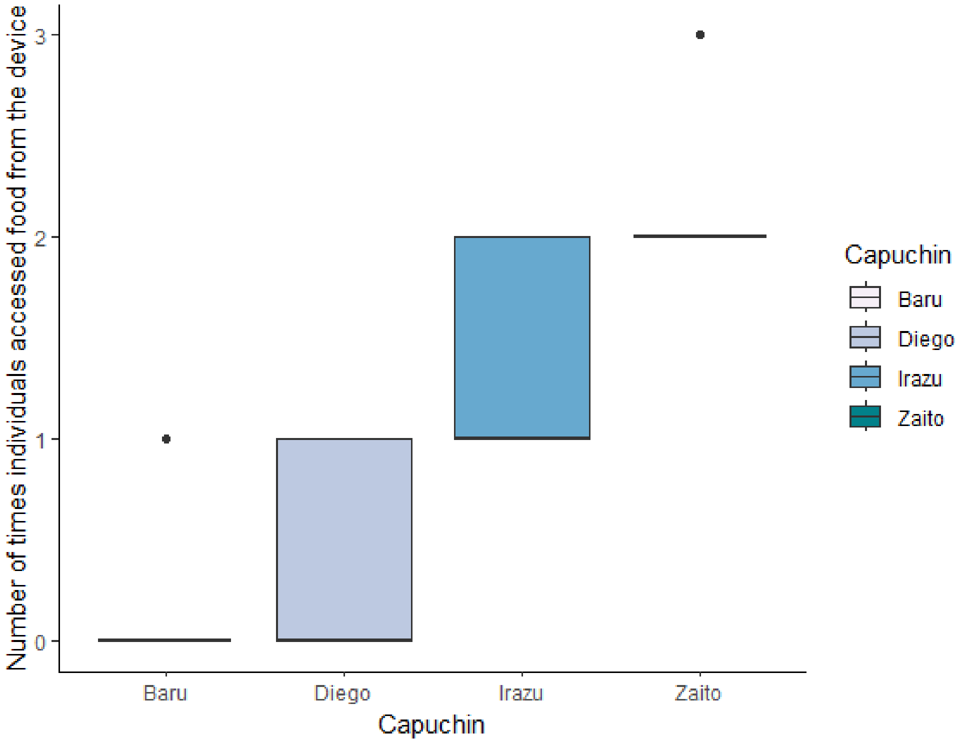

Figure 56: Number of times C. capucinus subjects accessed food from the device.

Kruskal-Wallis analysis indicated there was a statistically significant difference between adult and juvenile subjects and the number of times they accessed food from the device, adults accessed food more often $\chi^2 = 24.763$, df = 1, *p* = <0.001 (Figure 57).

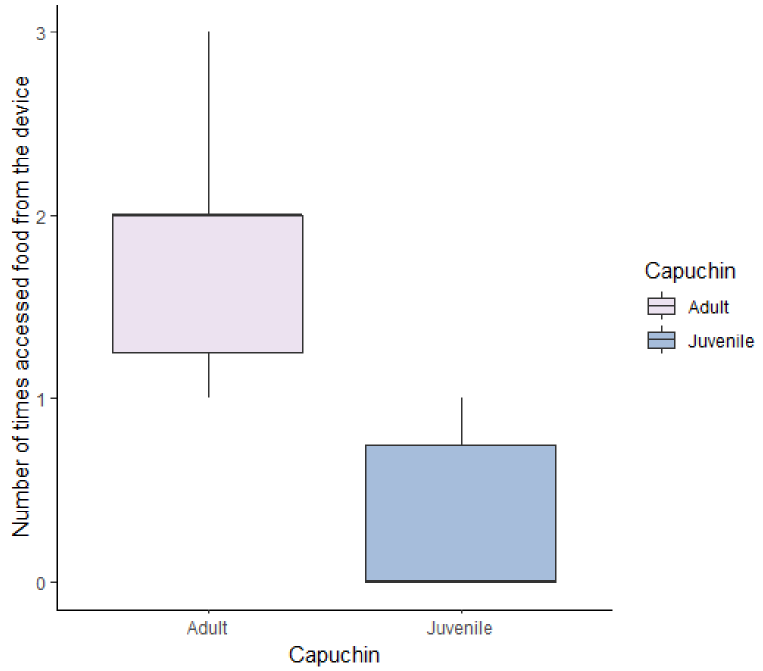

Figure 57: Boxplot of adult (n=2) and juvenile (n=2) access to food from the device.

Spearman's correlation determined the relationship between the number of trials and the number of times individuals accessed food from the device. There is a strong linear relationship between the number of trials and the number of times food was accessed (r_s = .94, n = 9, *p* = <0.01) (Figure 58).

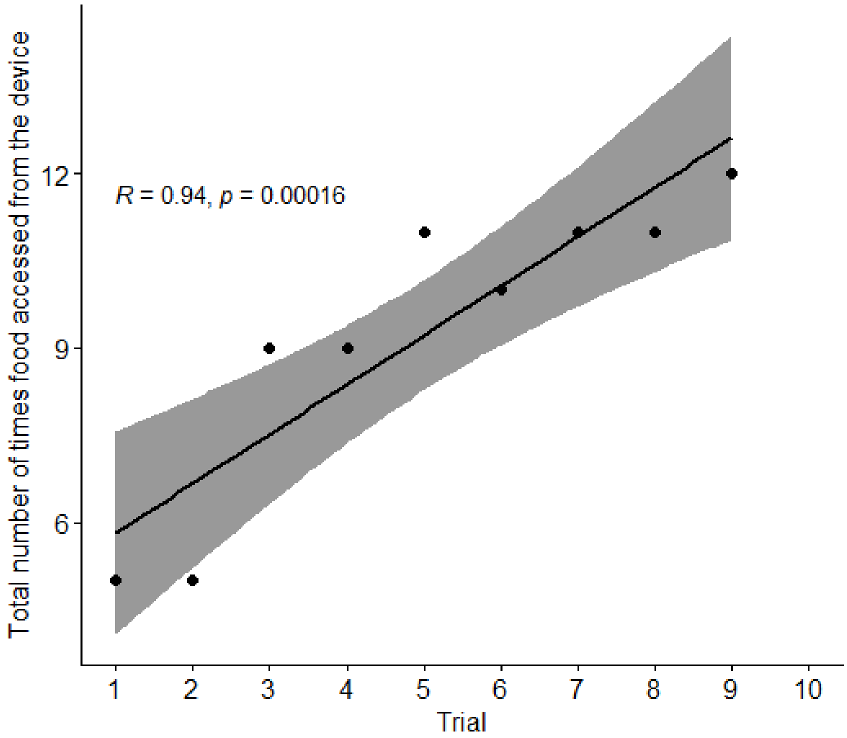

Figure 58: Spearman rank correlation - total number of times subjects accessed food from the device over the nine trials. The shaded area represents a 95% confidence interval.

3.4.5 Latency

A Kruskal-Wallis test indicated a statistically significant difference in latency of individual subjects to approach the device $\chi^2 = 22.594$, df = 3, $p = <0.001$. Further pairwise comparisons identified the following significant differences: Baru had a higher latency to approach the device than Irazu ($p = <0.05$) and Zaito ($p = <0.01$); Diego had a higher latency to approach the device than Irazu ($p = <0.01$) and Zaito ($p = <0.01$) and Irazu had a higher latency to approach the device than Zaito ($p = <0.01$) (Figure 59).

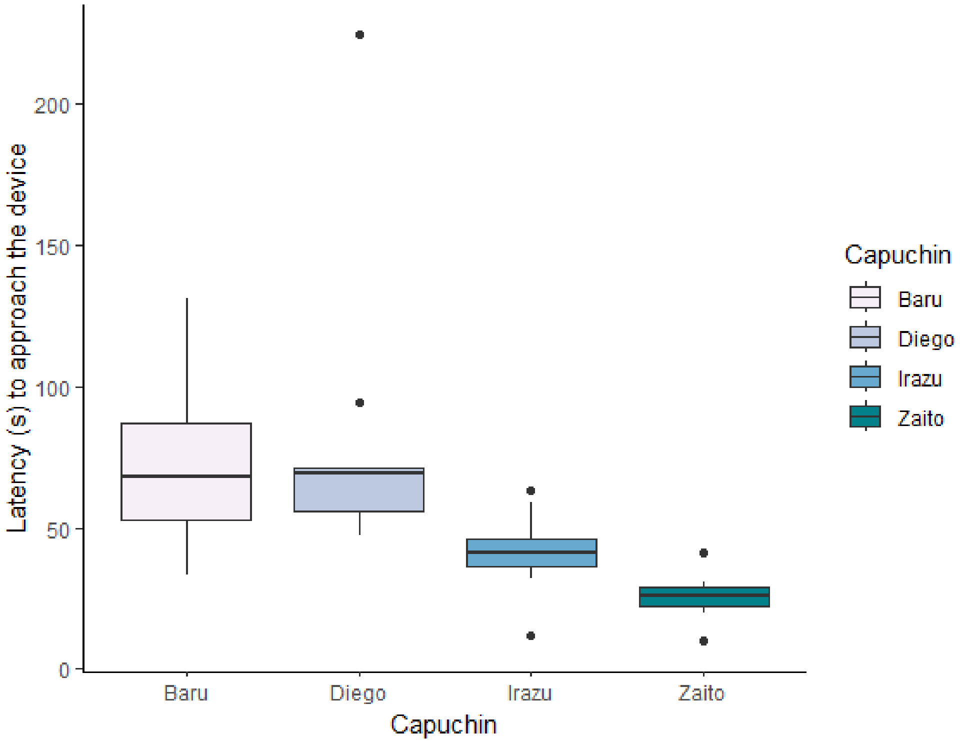

Figure 59: Latency (s) to approach the device for individual C. capucinus subjects.

Kruskal-Wallis analysis indicated there was a statistically significant difference between adult and juvenile subjects and latency to approach the device, adults were significantly quicker to approach the device $\chi^2 = 16.939$, df = 1, $p = <0.001$ (Figure 60).

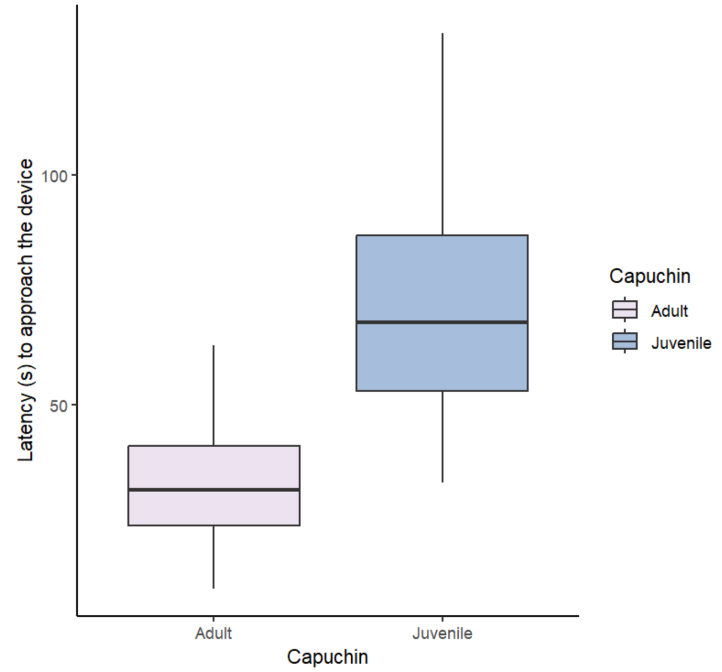

Figure 60: Latency (s) of adult (n=2) and juvenile (n=2) subjects to approach the device.

Spearman's correlation determined the relationship between the number of trials and latency of subjects to approach the device. There is a moderate linear relationship between the number of trials and latency to approach the device (r_s = .65, n = 9, *p* = 0.057) (Figure 61).

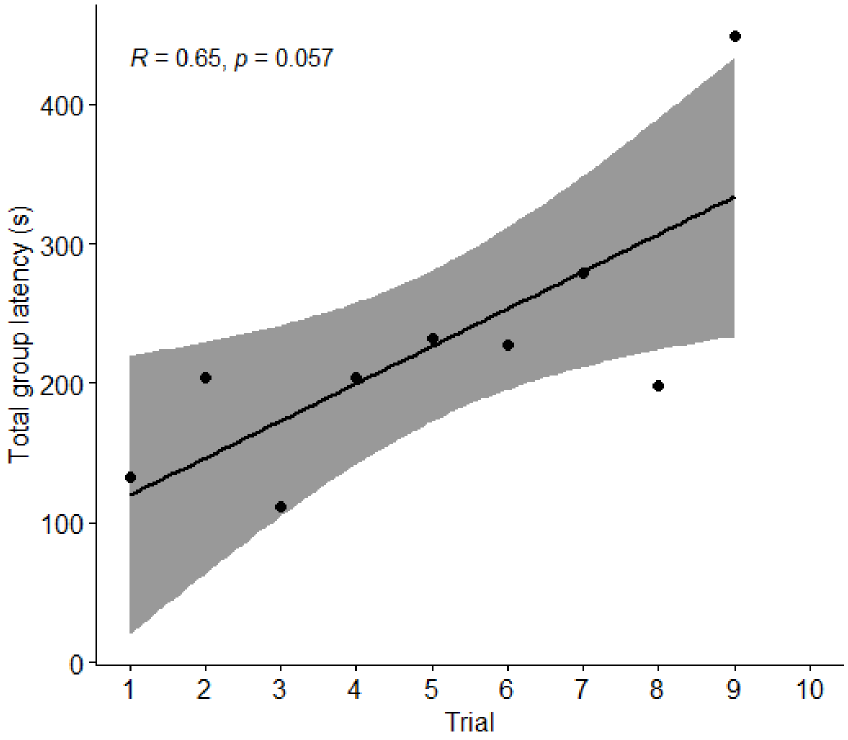

Figure 61: Spearman rank correlation - Latency (s) of subjects to approach the device over nine trials. The shaded area represents a 95% confidence interval.

4. Discussion

The aim of this study was to assess if captive *M. nigra* and *C. capucinus* subjects could spontaneously cooperate to solve a novel enrichment task and to determine if the introduction of novel cognitive enrichment tasks affects the activity budgets of the subjects. I found that the captive group of *M. nigra* were unable to spontaneously cooperate or intentionally coordinate actions to solve the task. Issues with the design of the device presented to the *C. capucinus* resulted in one individual being able to solve the task alone. While the overall activity budgets for both social groups were maintained, presentation of the cooperative enrichment device specifically increased locomotion in the group of *C. capucinus.*

4.1 Case study 1 - *M. nigra*

The *M. nigra* group did not cooperate to obtain a food reward from the novel cooperative enrichment device over the ten trials. However, there is a possibility that, if the trials had continued, unintentional cooperation might have occurred due to by-product selfish actions or presence-dependent rope-pulling. The *M. nigra* subjects showed sensitivity to partner presence, exhibiting significantly higher rates of rope-pulling when joined by others at the device. This supports the concept of presence-dependent cooperation (Albiach-Serrano, 2015) and aligns with the findings of Mendres and de Waal (2000) and Cronin, Kurian, and Snowdon (2005), who reported significantly higher pulling actions in *C. apella* and *S. oedipus* subjects when in the presence of a partner.

It is possible that the task used in the current study was too difficult for the subjects to understand, as they were unable to spontaneously solve the task by coordinating actions. Rope-pulling training could facilitate action-dependent cooperation (Hattori, Kuroshima and Fujita, 2005); however, it is suggested that further research is needed on captive groups of *M. nigra* to assess their ability to spontaneously cooperate.

Despite the cooperative task not being successfully solved, some individuals within the group continued to interact with the device over the ten trials, therefore suggesting it provided some level of stimulation. These findings concur with Clark *et al.,* (2019) observations reporting that subjects continue to interact with cognitive enrichment even when they are unable to solve the tasks presented, and justify the use of cognitive tasks for stimulation. The latency to approach the device decreased over the ten trials, however, it is important to note that the decline was not strongly correlated with the number of trials. The overall reduction in latency was driven by five subjects (Cheeketo, Elvis, Rafiki, Solina and Theo) and therefore does not represent the whole group. Maggie and Kashi had the highest latency to approach the device, this is may be attributed to other individuals dominating the device. Future studies should focus on investigating individual latency. I acknowledge that other factors not included in the statistical analysis models, such as weather or visitor number, may have contributed to the decrease in latency (Kendal, Coe and Laland, 2005). The location of the device could have affected use; the device was positioned within one indoor area of the enclosure. Therefore, variation in levels of engagement over the trials may have been affected by days where inclement weather conditions drove the subjects indoors. However, it is important to note that throughout the trials, subjects had access to two indoor enclosure areas, one with the device and one without, providing subjects with a choice.

Individuals spent varying amounts of time interacting with the device. As anticipated, based on existing literature, male subjects exhibited a higher frequency of approaching the device, spent more time interacting with it and pulled the ropes more frequently than females. Interestingly, Cheeketo, the dominant male of the group did not monopolise the enrichment device. Two males (Elvis and Rafiki) were the most frequent interactors with the device, the other subjects spent much less time interacting with the cooperative task. Differences in individual participation with cognitive enrichment has been reported in previous studies (Clark *et al.*, 2019; Jacobson *et al.*, 2019; Padrell *et al.*, 2022). Variation in participation could be influenced by factors such as, individual preference, personality and cognitive abilities (Padrell *et al.*, 2022). My results suggest it is important to consider individual differences when developing enrichment plans for captive primates. To address individual differences, it is suggested that separate cooperative enrichment devices could be set up in different locations within the enclosure. This would minimise competition for and the monopolisation of one single device, providing more than one opportunity for individuals to explore and interact with cognitive enrichment. In my study, a separate device may have provided the females with the opportunity to interact and cooperate away from the male subjects and creating more opportunity for partner choice.

Male subjects showed increased aggression towards the device compared to females; however, aggression levels remained consistent across the trials. Although enrichment is expected to reduce aggressive behaviour, cognitive challenges may elevate arousal and trigger emotional responses (Padrell *et al.*, 2022). Aggression directed at the enrichment device could stem from frustration due to the inability to understand and solve the cooperative task and therefore not being able to access the food reward. This suggests that the level of challenge might have exceeded the skills of the individuals within the group to spontaneously cooperate (Meehan and Mench, 2007; Lopresti-Goodman and Villatoro-Sorto, 2023). However, it is important to note that in the natural environment, *M.nigra* encounter challenges that require them to use complex cognitive skills including exploration, problem solving and cooperation. Therefore, I suggest research continues to inform the use of suitable cognitive enrichment devices to stimulate and provide opportunities for individuals learn and develop skills (Padrell *et al.*, 2022). Due to the low levels of aggression observed overall within this captive group, I concur with Jacobson et al. (2019) and apply caution in concluding that aggression is directly linked to and serves as an indicator of poor welfare. My findings can be used to inform future studies assessing the suitability of cooperative enrichment tasks, potentially expanding to include welfare assessments and physiological indicators of stress. It is important to note that no conspecific aggression was observed during interactions with the device, indicating no observable negative outcomes of aggression within the group. Although the presentation of novel cognitive enrichment did not lead to an increase in conspecific aggression in this study, it is recognised that, in addition to species-typical levels of social tolerance, there exists group-level variability (Jacobson *et al.*, 2019).

In contrast to the suggestion made by Padrell *et al.*, (2022) that primates quickly habituate to novel devices or tasks, my study observed an increase in the number of approaches, time spent interacting with the device, and the number of rope-pulls over the ten trials. There was no evidence of habituation. Notably, the food maze used in Padrell *et al.'s* (2022) study remained in place throughout their research. This included 12 days when the maze was loaded with food and 12 days when it was empty. This prolonged exposure may account for the habituation observed, which contrasts with my study where the device was removed in-between presentations. The increased levels of interaction reported in my study align with findings from Clark *et al.,* (2019) regarding gorillas' response to novel cognitive enrichment. However, additional trials and observations are necessary to comprehensively analyse habituation to the cooperation tasks.

Unlike several previous cooperative rope-pulling experiments, where partners choice is removed and cooperative behaviour is examined in controlled laboratory settings, my study presented subjects with a cooperation task within a social group context. Social pairing and interactions with the device correlated with levels of relatedness, and individuals with higher levels of relatedness interacted more frequently with the device. This suggests that there was a relatedness threshold for interactions, a notion supported by the findings of Chapais *et al.,* (1997). They reported that Japanese macaques demonstrated a relatedness threshold in nepotistic aiding behaviour. Alternatively, higher levels of interactions with the device could be explained by kin-biased social interactions linked to spatial associations (Van Belle, Estrada and Di Fiore, 2014). Molesti and Majolo (2016) conducted research on free partner choice in wild Barbary macaques, revealing that dominance status, sex, age, and temperament influenced partner choice and subsequent successful cooperation. These factors might have similarly impacted the interactions of *M. nigra* with the device. The small group size in this case study, is a constraint on the reliability of these findings. Further research is necessary to explore nepotistic partner choice and intragroup spatial associations in cooperative tasks.

This group of *M. nigra* had no previous experience of cooperative enrichment tasks, interaction with the cooperative enrichment device was on a voluntary, individual choice basis. Two female subjects showed minimal interest in the device, as well as indicating a sex difference, this may also be related to individual responses to enrichment, which is an important consideration (Jacobson *et al.*, 2019). Existing research suggests that whole group participation is considered uncommon in voluntary tasks (Whitehouse *et al.*, 2013). It is important to explore possible explanations for these individual differences (Kemp, 2023). One explanation may be that these female subjects experienced neophobia towards the unfamiliar device (Kemp, 2023). Although there were no clear behavioural indicators that the device compromised their welfare, this is a point to consider in future studies. An alternative explanation is that the two female subjects possibly took advantage of other group members being distracted with the device to engage in other behaviours. Further behavioural observations would be necessary to investigate these potential explanations.

Comparative activity budgets indicate that the device had no overall effect on the group's expression of prosocial behaviour, foraging and feeding behaviour, locomotive behaviour or aggression directed at conspecifics. The dominant male, Cheeketo expressed more aggressive behaviour when the device was present, in contrast, Elvis, the second eldest male, expressed less aggression towards others when the device was present. It was predicted that prosocial behaviour would increase in the presence of the enrichment device, however, the results of my study contradict research by Smith (2013), who reported an increase in friendly behaviours of captive *M. nigra* in the presence of environmental enrichment. As the overall activity budget of the captive group was maintained, there are no obvious behavioural indicators that the device compromised, or negatively affected welfare. Further research investigating other indicators of positive and negative states, for example, recording observed events of subtle forms of communication between conspecifics in response to novel cooperative enrichment, could be used to further assess the impact of such enrichment on the welfare of captive *M. nigra.*

I acknowledge that training phases could be used in captive settings to encourage cooperative behaviour (Marshall-Pescini *et al.*, 2016), providing individuals with the opportunity for cognitive development and promoting prosocial behaviours. Therefore, I propose continuing research assessing the suitability of cooperative enrichment tasks, so that these tasks become integral to the husbandry practice for this critically endangered species.

4.2 Case study 2 - *C. capucinus*

The dominant male of the group used an alternative strategy to access the food reward, which was attributed to a design flaw in the apparatus. It was intended that if one individual pulled on one end of a rope alone, the rope would pull through the device. However, due to safety restrictions, knots were used on the ends of the rope to prevent the rope being pulled completely through into the enclosure. Because the rope remained attached to the device, the dominant male was able to swivel the device closer to the enclosure, extend his arm through the mesh enclosure wall, and pull on the section of the rope outside the enclosure. Consequently, modifications to the device are necessary for repeated studies investigating the cooperative capabilities of the group.

While the device did not serve as a cooperative task for the group, it did provide stimulating cognitive enrichment and opportunities for choice and exploration of a novel object. The adult male was always the first to approach and interact with the device, this could be evidence of the other subjects deferring to his dominance and monopoly over the device (Perry, 1997, 1998; Jack and Fedigan, 2004). After successfully pulling the device and accessing the food, the dominant male would be joined by the adult female, indicating that this dyad engages in reciprocal food sharing, a form of prosocial behaviour. The explanation for this prosocial behaviour may be explained by attitudinal reciprocity, which is said to be determined by social bonding (Schino and Aureli, 2010b).

In this case study, the latency to approach the device moderately increased over the ten trials, possibly indicating habituation to the device. It is important to note however, that the increase in latency is driven by the two juveniles (Baru and Diego) and therefore does not represent of the whole group. As suggested previously, detailed analysis of individual latency is needed. This will be incorporated into ongoing research. As well as taking longer to approach the device, the juvenile subjects spent less time interacting with it. Mainly, juveniles invested more time in proximity, observing the adult subjects. A possible explanation for this observation is that the juveniles opted to watch and learn from the adults before engaging with the device themselves (Ottoni and Izar, 2008). However, Perry (2020) proposes that juvenile *C. capucinus* exhibit less neophobia than adults during extraction-based foraging behaviour. Therefore, the juvenile proximity behaviour might be explained by their deference to the dominance rank of the adults and their monopolisation of the device (Vogel, Munch and Janson, 2007). The proximity behaviour of the juveniles may also align with the producer-scrounger dynamics in social foraging strategies (Di Bitetti and Janson, 2001).

Comparative activity budgets indicate a significant increase in locomotion when the device was present, indicating the device served as a stimulus for the subjects. Webb and Schapiro (2023) suggest increased locomotion can be used as an indicator of improved welfare, although they highlight the relationship between locomotion and welfare is nuanced and therefore, I recommend that future research needs to investigate the subtleties and complexities of the relationship between locomotion and welfare.

Over the nine trials, the subjects increased the time spent interacting with the device and the number of rope-pulls, as with the first case study, there was no evidence of habituation. Despite the device being pulled close enough to access the food reward, the subjects continued to pull on the ropes, demonstrating continued explorative behaviour.

Social pairings and interactions at the device were not analysed for the group of *C. capucinus,* it is recommended that a larger group with more unrelated individuals is needed to investigate explanations of partner choice. The overall activity budget of the group was maintained and there was no evidence that the device negatively impacted the welfare of the group. However, I suggest that future research should consider investigating more subtle forms of welfare indicators for example: vocalisations, body posture, and facial expressions in addition to the use of the comparative activity budgets. More detailed behavioural diversity measures could provide a more robust approach to assessing primate welfare when novel enrichment is introduced to the captive environment (Miller *et al.*, 2021). Therefore, further research investigating the cooperative behaviour and the suitability of cooperative cognitive enrichment is recommended for this captive group of *C. capucinus.*

4.3 Limitations and future directions

Although I believe that both case studies provide insights into behavioural responses to novel cognitive enrichment, limitations need to be acknowledged. Both case studies are based on single social groups, however while it is common with zoo-based research (Jacobson *et al.*, 2019) it limits the generalisability of the behavioural responses recorded. Utilising single social groups results in repeated observations of individuals, can lead to pseudoreplication, which can affect the independence of the data. It is also important to acknowledge that as with most zoo-based studies, the social grouping of captive primates is a limiting factor as they often differ significantly from those observed in the wild (Price and Stoinski, 2007). In my research, the ratio of males to females and small group sizes are limiting factors of the studies. Other limitations of my study include the confounding variables: time of day, visitor number and weather conditions, which were not controlled in the statistical analysis models and should be included in future studies.

I acknowledge that in some instances, specific individuals drive the significant relationships identified and that there were individual differences in the level of interaction with the devices (Izzo, Bashaw and Campbell, 2011; Costa, Sousa and Llorente, 2018; Kemp, 2023). Therefore, I suggest investigating individual effects in future studies. Assessing the suitability of cooperative enrichment by testing all of the behaviours included in my analysis models, may not necessarily be meaningful and appropriate. Instead, future studies should concentrate on investigating and analysing the nuances of behaviours, specifically, prosocial interactions, locomotion, and aggression as indicators of welfare.

The devices were designed and based on previous pulling paradigm research, however, the design of each was determined by enclosure layout, specifications and observer access. Necessary adaptions have been identified and planned for the device used in the *C. capucinus* case study and will be used in future research with the group at Newquay Zoo. The simplicity of this device design means it can easily be adapted to individual enclosure specifications and rolled out across zoos for comparative research. A notable advantage of the rope-pulling paradigm is its flexibility allowing limitless variations in its basic concept (Jacobs and Osvath, 2015). The device used in the first case study proved to be too difficult for the skill level of the *M. nigra,* this is a common challenge in cooperation research (Marshall-Pescini *et al.*, 2016). Future studies should consider incorporating the use of solo-enrichment pulling devices as a control. This approach can help reinforce individual pulling actions before introducing cooperation tasks. However, it is important to acknowledge that this might contribute to challenges in distinguishing between intentional and accidental cooperation, as well as assessing the impact of action-dependence and presence-dependence rope pulling (Albiach-Serrano, 2015; Jensen, 2016).

While incorporating prior training restricts the investigation of spontaneous cooperation, it should be considered in cases where promoting prosocial collaborative behaviour is a desirable outcome. In future zoo-based cooperation research, training could be used to ensure that the subjects comprehend the task, however, it is suggested that over-training should be avoided, as it can lead to inflating estimations of prosocial behaviour (Marshall-Pescini *et al.*, 2016).

4.4 Conclusion

Despite the absence of cooperation during the interactions with the enrichment device in both case studies, this study provides support for using novel tasks as cognitive enrichment for captive *M. nigra* and *C. capucinus.* Despite the limitations addressed, my results can add to existing literature addressing the suitability of novel cognitive enrichment for captive primates and can be used to inform future studies.

I urge continued research and the integration of cooperative enrichment into evidence-based husbandry practice and make the following recommendations for consideration: a) integrate novel cooperative tasks into routine enrichment plans to stimulate the cognitive abilities of *M. nigra* and *C. capucinus.* These tasks should encourage problem-solving, social interactions and promote the development of cooperative behaviour; b) systematically monitor the effects of cooperative enrichment tasks to assess their impact on the welfare of captive *M. nigra* and *C. capucinus;* c) foster collaboration between researchers and zookeepers to facilitate the exchange of information; d) develop educational programs to raise awareness of the importance of cognitive enrichment linked to conservation of these species.

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6. Appendix

Appendix 1: Activity budget ethogram for case study 1 – *M. nigra*

Ethogram for Black Crested Sulawesi Macaque (*Macaca nigra)* (Baker, 2012)

	Broad Category	**Detailed Category**	**Definition**
State Behaviours	Active	Locomotion	Any movement around the environment. Includes walking, running, climbing, jumping and swinging. Movement can be bipedal or quadrapedal.
		Foraging	Actively looking for food, or searching for food using forelimbs.
		Feeding/drinking	Consuming food items.
	Social	Contact	Sitting in contact with another animal. This may involve more than one animal in a social 'huddle'.
		Play	Wrestling, chasing another animal
		Aggression	Threat gestures (body posture) or physical aggression towards another animal including, lunge, slap, grab, bite (focal animal initiating or receiving aggression)
		Autogroom	Picking through own fur with fingers
		Allogroom	Picking through fur of another animal with fingers
	Interaction (Environment)	Interaction with Environmental Enrichment (EE)	Any interaction with Enrichment items that are put in the enclosure
		Interaction with Enclosure features (EN)	Any interaction with enclosure features that is not food related.
	Rest	Alert	Animal is stationary but alert to surroundings
		Rest	Animal is stationary with eyes closed, does not respond quickly to surrounding stimuli
	Out of view		Animal is not in sight
	Other		Any other behaviour not previously defined
Event behaviours		Scratch	Repetitive raking of the skin using fingers or feet
		Yawn	Gaping movement of the mouth. Head is tossed back when mouth is fully open.
		Grimace	Silent bared-teeth
		Lipsmack	Smacking lips together (with scalp retraction)

Displace	Focal animal moves towards animal *x* and animal *x* moves away
Displaced	Animal *x* moves towards focal animal and focal animal moves away
Self Directed Behaviour (SDB)	Any self directed behaviour which is repetitive with no obvious function

Key:

🟨 = behaviours grouped as ‘prosocial’ for analysis

Appendix 2: Video analysis ethogram for case study 1 – *M. nigra*

Video analysis ethogram for Black Crested Sulawesi Macaque (*Macaca nigra)*

Category	**Definition**
Interacting with the device	Touching the device with any part of the body, sitting on the device
Approach	Move towards device with purpose, looking at the device whilst within reach of the device
Rope-pull	Pull of the rope towards the individual, using any part of the body
Aggression towards the device	Shaking the device, jumping up and down on the poles of the device
Latency	Time between starting the observation and an individual first approaching/interacting with the device

Appendix 3: Activity budget ethogram for case study 2 - *C. capucinus*

Ethogram for White-Throated Capuchin (*Cebus capucinus*)

Broad Category		Detailed Category	Definition
State Behaviours	Active	Locomotion	Any movement around or across the enclosure environment. Includes walking, running, climbing, jumping and swinging (Mallott et al., 2016). Movement can be bipedal or quadrapedal.
		Foraging	Time devoted to actively looking for food items within the enclosure, may include sniffing or manipulation of floor substrates to locate food items (Mallott et al., 2016; Gunst et al., 2010).
		Feeding/drinking	Handling and consuming food items (Gunst et al., 2010), often using teeth, hands, or feet to forcefully pull food items, sometimes pulling with arms or even the whole body (Janson and Boinski, 1992). May smash food on a surface or use tools to gain access to items such as nuts (Canale et al., 2009). Taking water into the mouth using hands or bending the head down to access water (Bezerra et al., 2011).
		Physical engagement/manipulation of cooperative enrichment (CE)	Animal shows interest in cooperative enrichment device by attempting to use it or by trying to manipulate it in some way
		Physical engagement/manipulation of environmental enrichment (EE)	Animal shows interest in environmental enrichment by attempting to use it or by trying to manipulate it in some way
	Abnormal	Stereotypic behaviours	Any behaviour performed which is repetitive, unvarying, and apparently functionless (Mason, 1991). Examples in capuchins include: Stereotypic pacing - repetitive walking of the same area within the cage,

			or repetitive brachiation along the same route; Head twirling - repetitive circular movements of the head; Hair pulling - repeatedly pulling out hair from the body using a hand or foot (Pomerantz et al., 2012; Pomerantz et al., 2013).
State Behaviours continued	Social	Sharing food (FS)	Conspecifics pass the same food item to one another whilst both consuming it (Bezerra et al., 2011).
		Allogrooming	One animal manipulating the skin or hair of a conspecific, either with their hands and/or with their mouth (Perry et al., 2008).
		Social play	Wrestling, chasing, or being chased by another individual (Visalberghi and Guidi, 1998; Paukner and Suomi, 2008).
		Social contact	Sitting/laying in contact with another animal. This may involve more than one animal in a social ‘huddle’.
		Social anointment	Tow or more individuals involved in crushing and spreading a foreign substance on their fur with hands or feet and rubbing on each others fur (Baker, 1996). This substance can be vegetal (plant material, food items)
	Solitary behaviour	Solitary play	Includes: Object play - the manual exploration and manipulation of any enrichment or structural items provided within the animal's enclosure, may include banging items (could be food) on the floor or any surface within the enclosure, or rubbing them between their palms; Arboreal play - quick, acrobatic, and/or exaggerated locomotion such as somersaults or swinging from their own tail (Visalberghi

			and Guidi, 1998; Paukner and Suomi, 2008).
		autogrooming	One animal manipulating their own skin or hair, either with their hands and/or with their mouth (Perry et al., 2008).
		Solitary resting	Sitting/laying alone
		Solitary anointment	Individual crushing and spreading a foreign substance on their fur with hands or feet (Baker, 1996). This substance can be vegetal (plant material, food items)
	Agonistic	Aggression	Including mild forms such as open-mouthed threats or threat faces, and more severe forms such as chases, lunges, and grapples (Perry et al., 2008; Vogel et al., 2007).
	Other	Out of sight	Animal is not visible
Event behaviours		Vocalisation	Including mild forms such as open-mouthed threats or threat faces, and more severe forms such as chases, lunges, and grapples (Perry et al., 2008; Vogel et al., 2007).
		Yawning	Opening the mouth widely and performing a deep inhalation, apparently involuntarily (Bezerra et al., 2011).
		Scratch	Repeated rubbing of an area of the body using a hand or foot (Bezerra et al., 2011).
		Displaced	Animal *x* moves towards focal animal and focal animal moves away

Appendix 4: Video analysis ethogram for case study 2 – C*. capucinus*

Video analysis ethogram for White-Throated Capuchin (*Cebus capucinus)*

Category	**Definition**
Interacting with the device	Touching the device with any part of the body
In proximity	Subject within 1 metre of the device, looking at the device or individual interacting with the device
Rope-pull	Pull of the rope towards the individual, using any part of the body
Access food	Subject retrieving food items from the device
Latency	Time between starting the observation and an individual first approaching/interacting with the device

Appendix 5 Additional results

M. nigra activity budgets

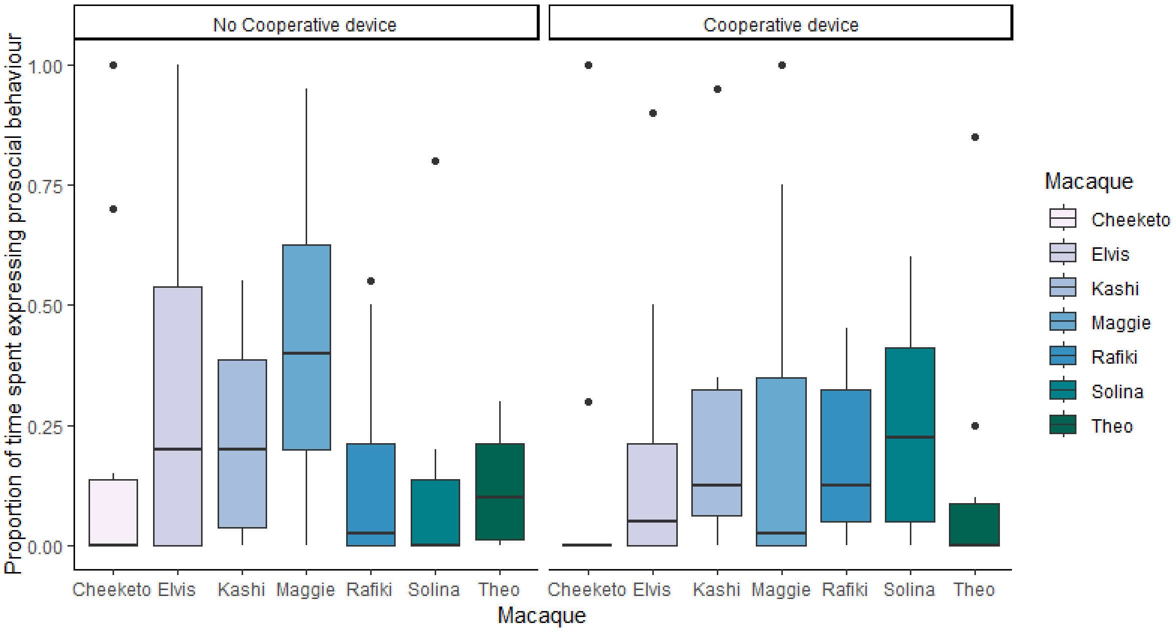

Figure 62: Proportion of time M. nigra subjects spent expressing prosocial behaviour during non-presentation and presentation of the device.

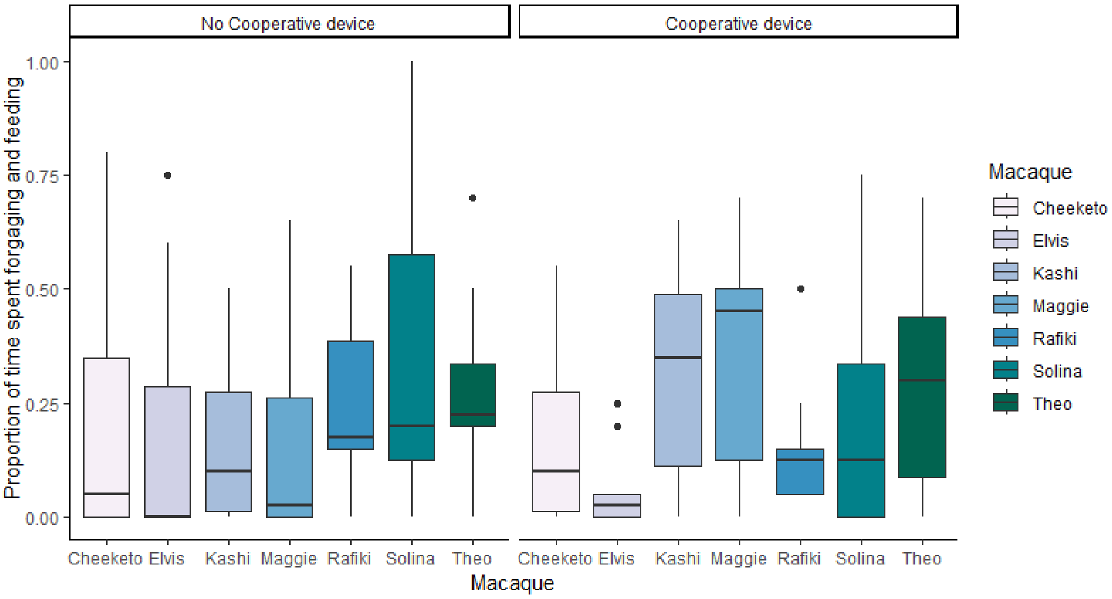

Figure 63: Proportion of time M. nigra subjects spent foraging and feeding during non-presentation and presentation of the device.

M. nigra video analysis

Figure 64 illustrates how the time spent interacting with the device varied over the ten trials for each subject. A reduction in the amount of time spent interacting with the device was evident in trial 3. Elvis spent the longest amount of time interacting with the device during trial 7. The amount of time Theo spent interacting with the device increased over the number of trials. Elvis, Rafiki, Solina and Theo all spent time interacting with the device in all 10 trials.

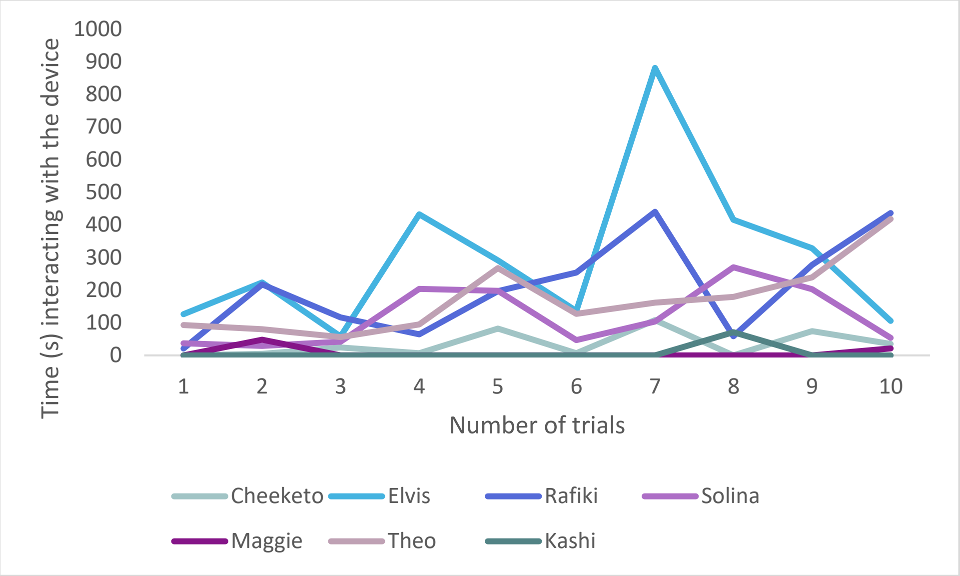

Figure 64: Time (s) M. nigra spent interacting with the device over the ten trials.

Figure 65 illustrates how the number of aggressive acts towards the device varied over the ten trials. Elvis and Cheeketo expressed the highest number of aggressive acts. Elvis expressed the highest number of aggressive acts towards the device during trial 4. Maggie, Kashi and Theo did not express any aggression towards the device.

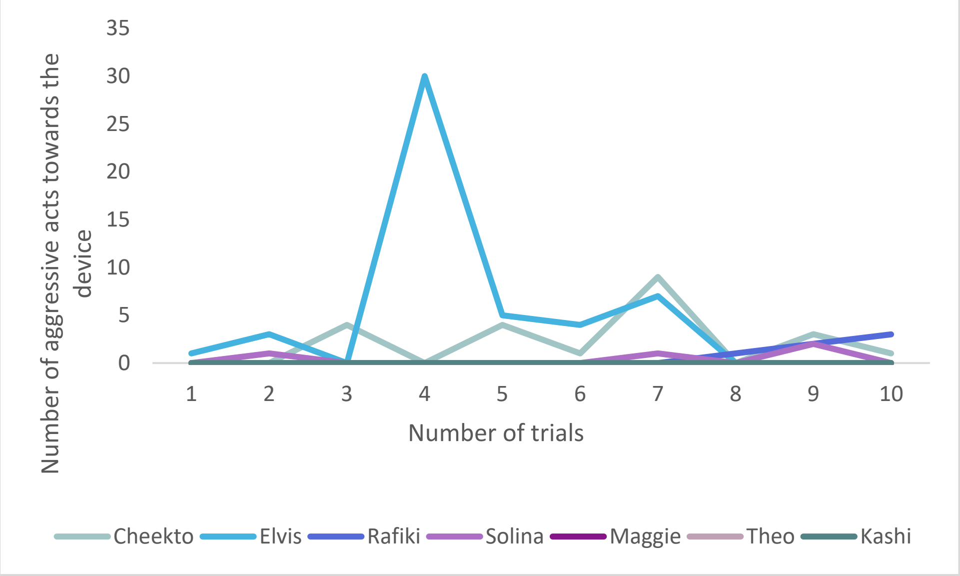

Figure 65: Number of aggressive acts towards the device over the ten trials.

Figure 66 illustrates how the number of approaches to the device varied over the ten trials. Elvis made the highest number of approaches during trials 7 and 10. Elvis, Rafiki, Solina and Theo all approached the device in all 10 trials.

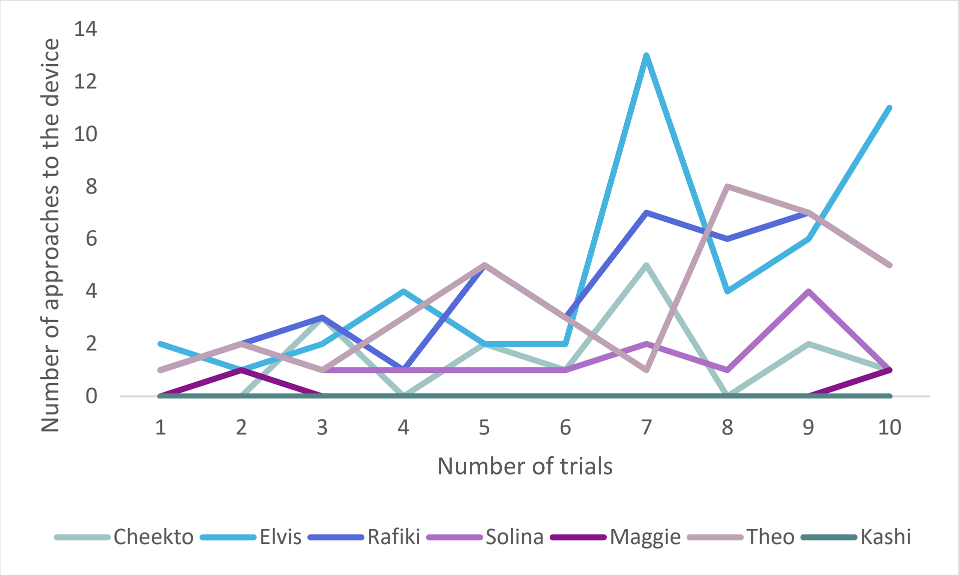

Figure 66: Number of approaches to the device over the ten trials.

Figure 67 illustrates how the number of rope-pulls varied over the 10 trials. Neither Cheeketo or Maggie pulled the ropes of the device during any trial. Elvis pulled the ropes more often during trial 7, and did not pull the ropes during trial 9 and 10. Rafiki pulled the ropes in each trial except for trial 1.

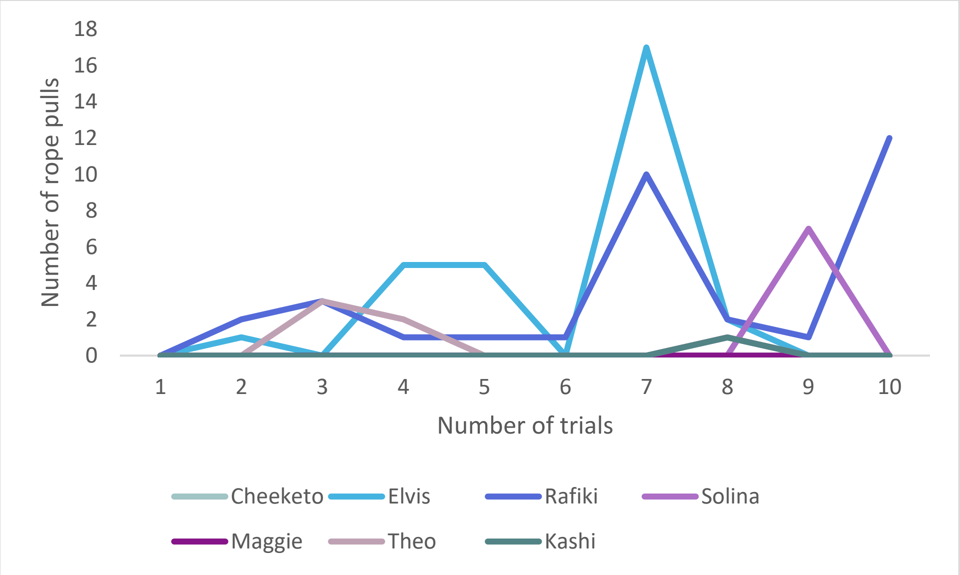

Figure 67: Number of rope-pulls over the ten trials.

Figure 68 illustrates the latency of subjects to approach the device over the ten trials. Cheeketo, had the highest latency score out of the male subjects. Solina’s latency was consistent over trials 3, 5, 6,7 and 8. Kashi and Maggie were removed as they both only approached the device once over the ten trials.

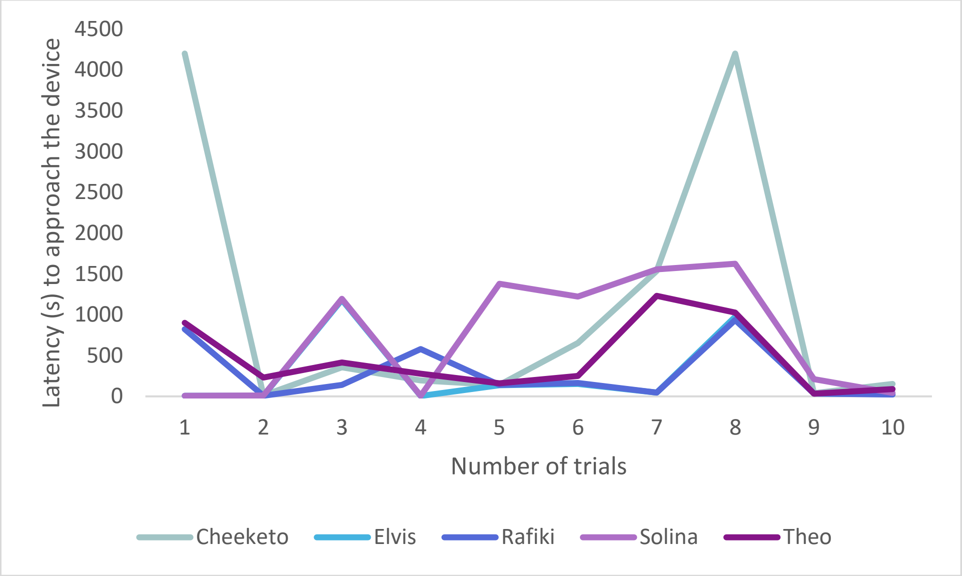

Figure 68: Latency (s) of individua macaques to approach the cooperative enrichment device over the ten trials.

C. capucinus activity budget

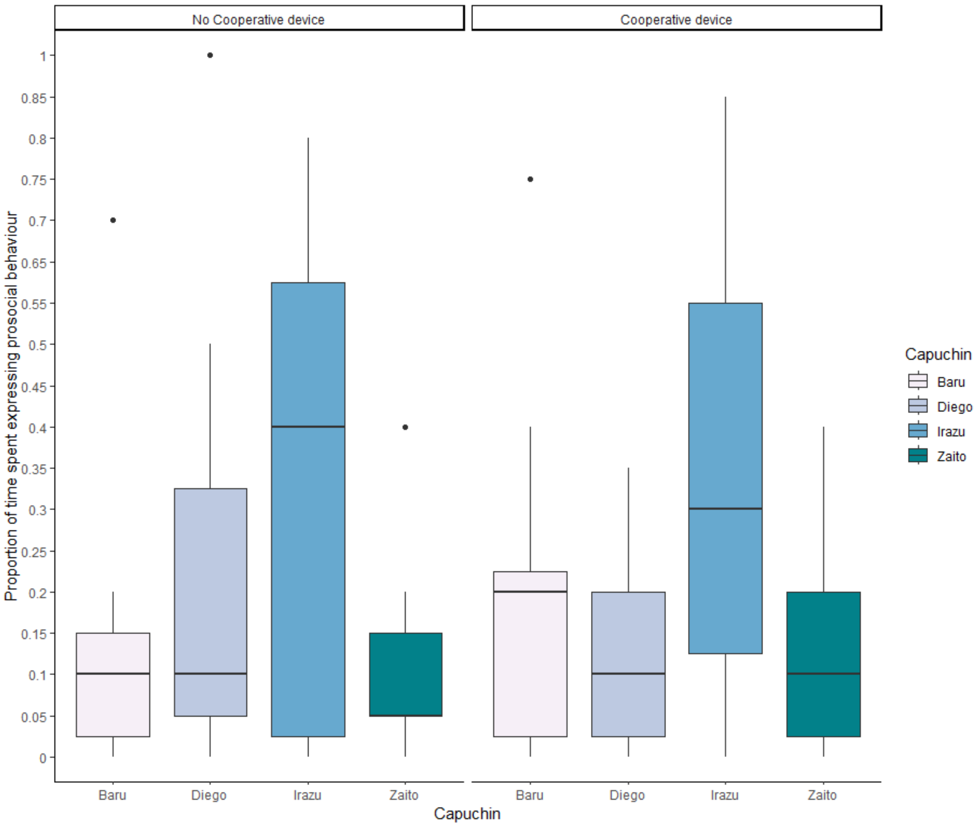

Figure 69: Proportion of time C capucinus subjects spent expressing prosocial behaviour during non-presentation and presentation of the device.

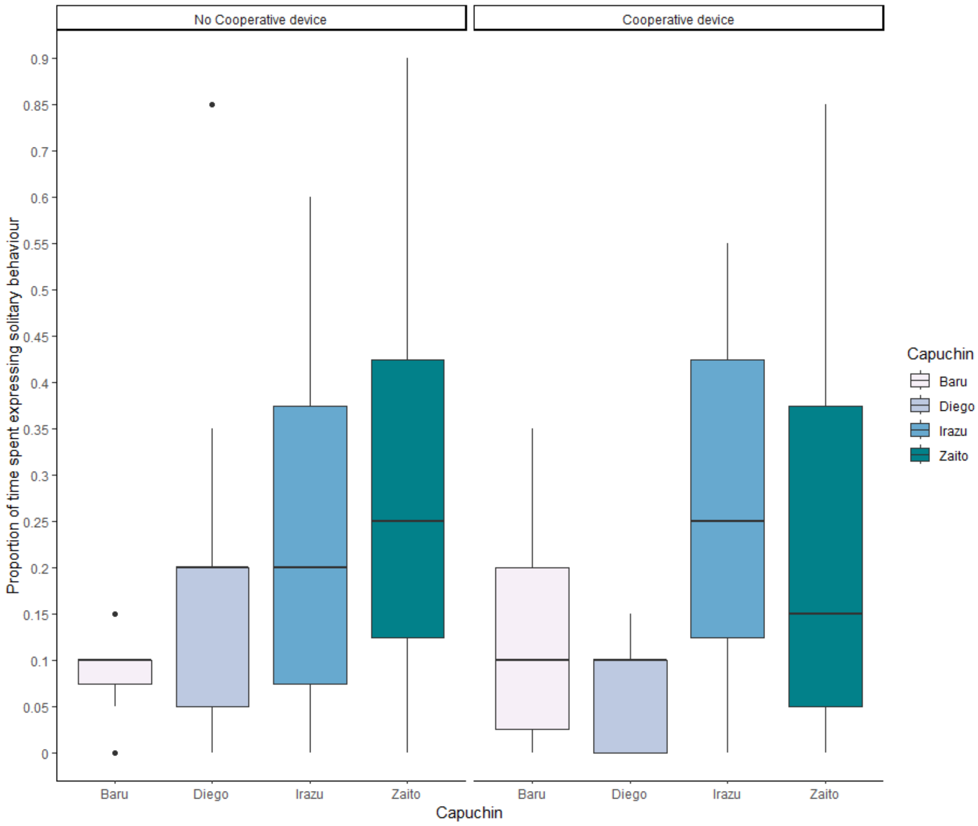

Figure 70: Proportion of time C. capucinus subjects spent expressing solitary behaviour during non-presentation and presentation of the device.

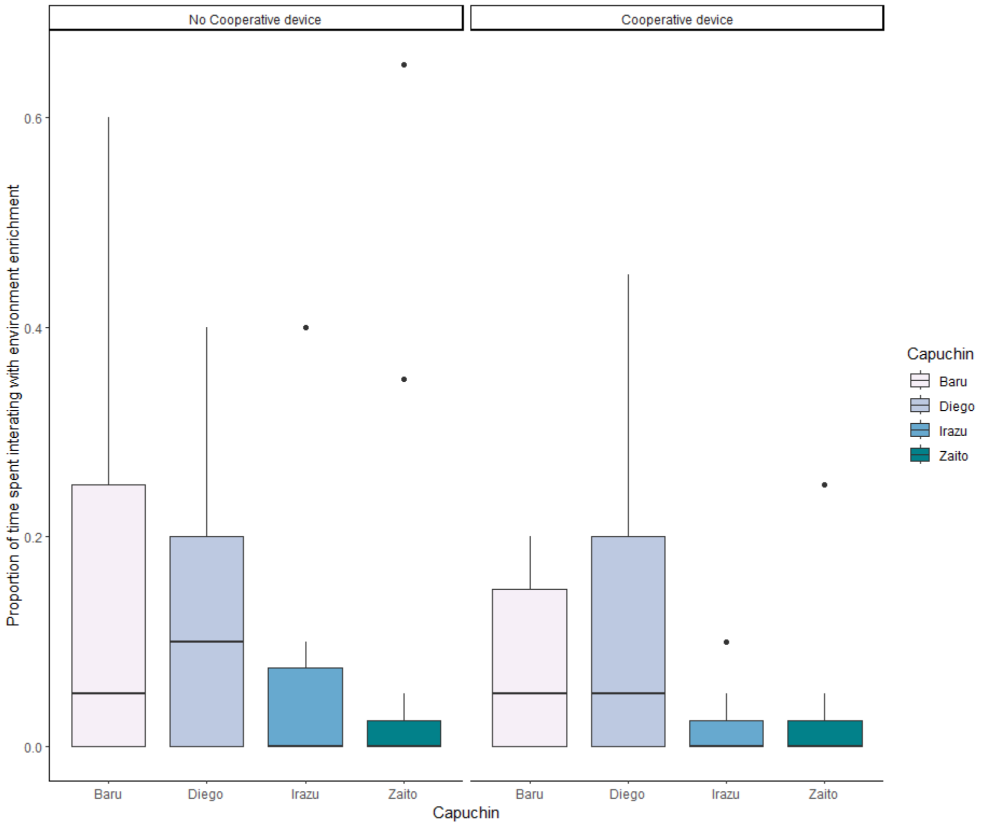

Figure 71: Proportion of time C. capucinus subjects spent interacting with other environmental enrichment within the enclosure during non-presentation and presentation of the device.

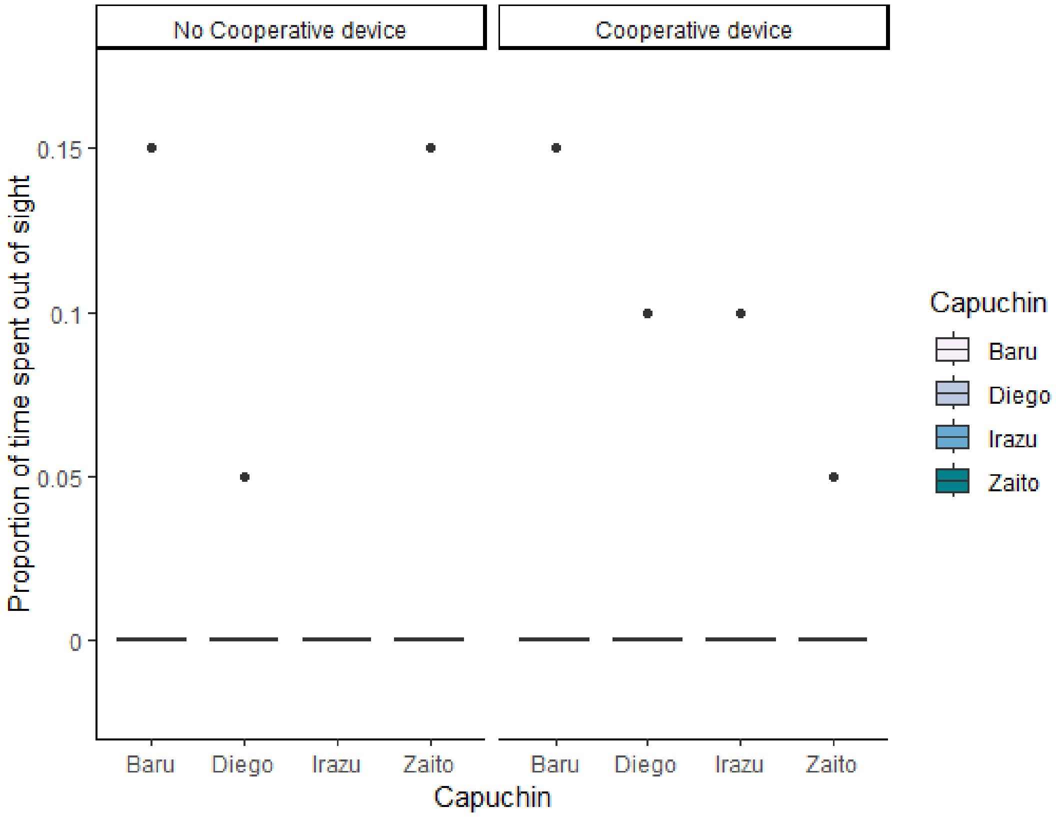

Figure 72: Proportion of time C. capucinus subjects spent out of sight during non-presentation and presentation of the device.

C. capucinus video analysis

Figure 73 illustrates how the proportion of time subjects spent in proximity to the device varied over the nine trials. The highest proportion of time spent in proximity was during trial three and five.

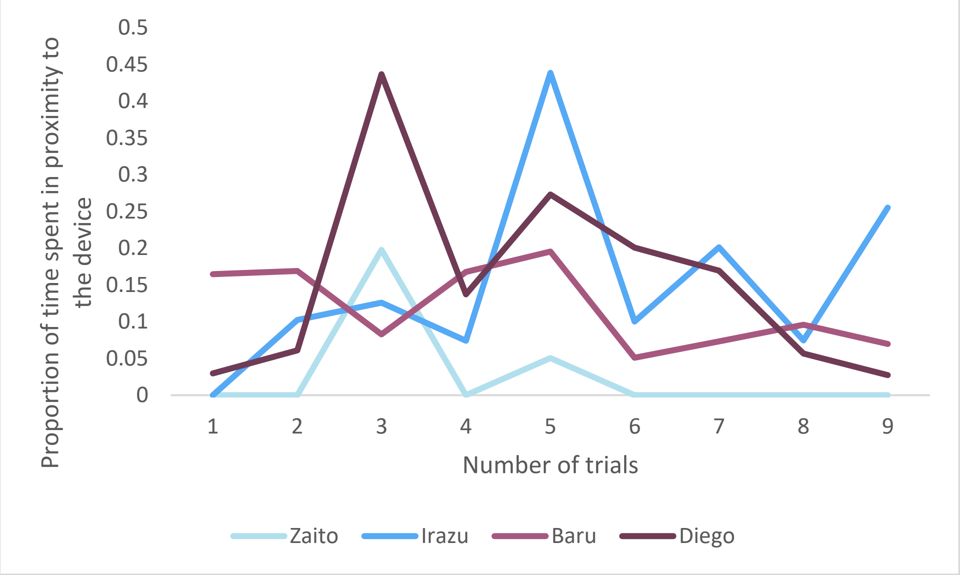

Figure 73: Proportion of time C. capucinus spent in proximity to the device of the nine trials.

Figure 74 illustrates how the proportion of time subjects spent interacting with the device varied over the nine trials. The highest proportion of time spent interacting with the device was during trial three. The dominant adult male and adult female spent more time interacting with the device that the two juvenile males over the nine trials

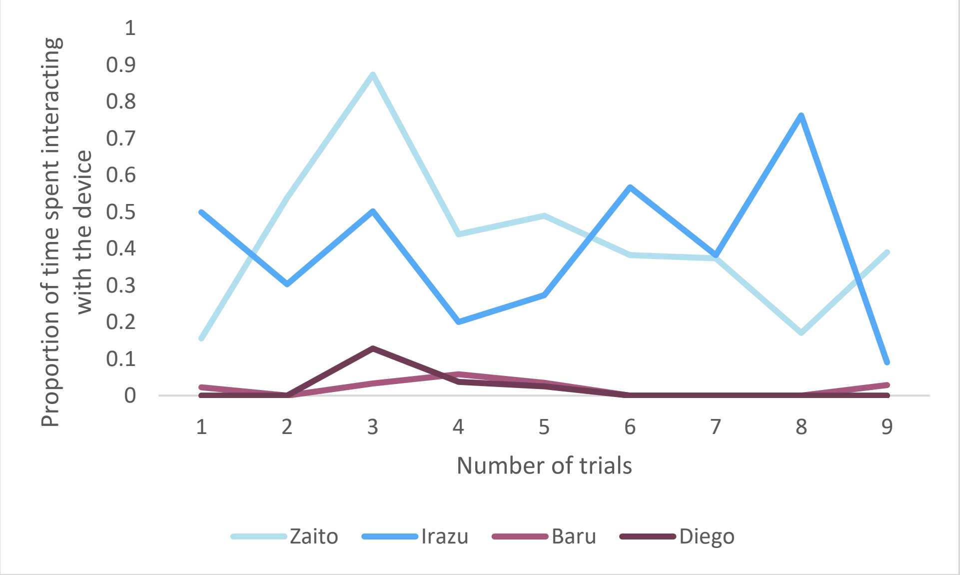

Figure 74: Proportion of time C. capucinus spent interacting with the device over the nine trials.

Figure 75 illustrates the number of rope-pulls over the nine trials for each subject. Baru only pulled the ropes in trial 9, Diego only pulled the ropes in trial 3. Zaito is the only subject to pull the rope in all nine trials.

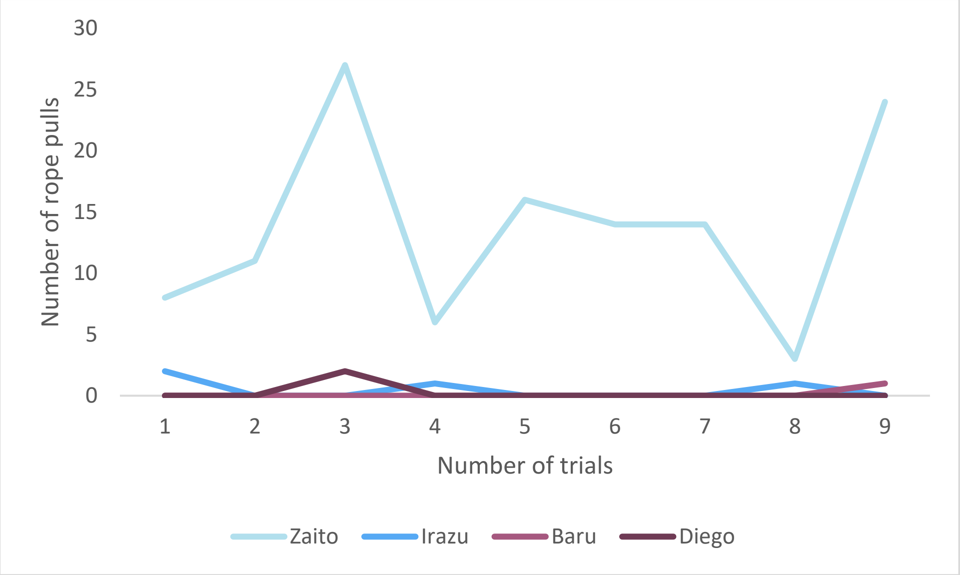

Figure 75: Number of rope-pulls for each subject over the nine trials.

Figure 76 illustrates the number of times subjects accessed food from the device over the nine trials. Both Zaito and Irazu accessed food during every trial. Baru only access food during trial 3 and 4 and Diego only accessed food during trial 3, 4 and 5.

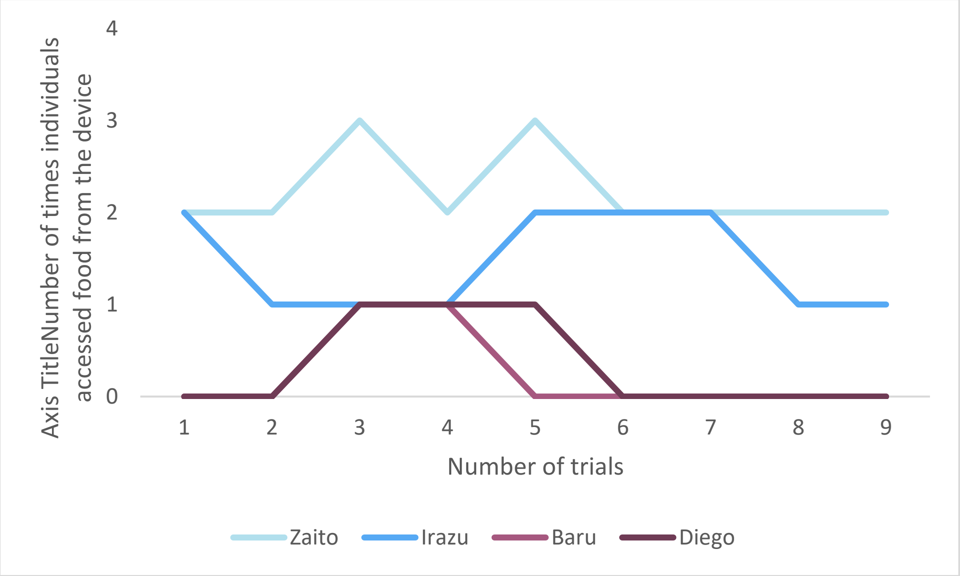

Figure 76: Number of times individual subjects accessed food from the device over the nine trials.

Figure 77 illustrates the latency of subjects to approach the device over the nine trials. Zaito and Irazu were quicker to approach the device than Baru and Diego. Both Baru and Diego took longer to approach the device during trial 9.

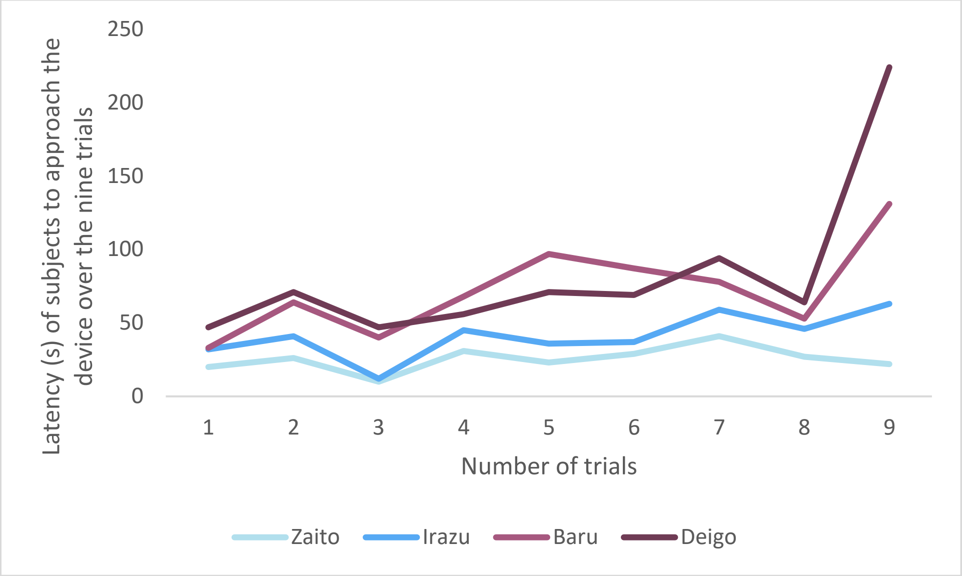

Figure 77: Latency (s) of individual subjects to approach the device over the nine trials.