

2017

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Bee, K. (2017) 'The long term effects of social deprivation on black-capped capuchins (*Sapajus apella*) rescued from the primate pet trade', *The Plymouth Student Scientist*, 10(2), p. 4-27.

<http://hdl.handle.net/10026.1/14157>

The Plymouth Student Scientist
University of Plymouth

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The long term effects of social deprivation on black-capped capuchins (*Sapajus apella*) rescued from the primate pet trade.

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Abstract

Captivity is often physically and psychologically damaging to primates, who have complex ethological and social needs. It is widely agreed that primates do not make suitable domestic pets, however it is still legal to keep some species of primates as pets in the UK. The effects of the exotic pet trade on primate welfare are poorly documented. It is extremely likely that it will be detrimental towards their physical and mental health, especially when kept in isolation from other primates, but there is little evidence to show the long-term implications of social deprivation. This study observed the long term-effects of social isolation on black-capped capuchins (*Sapajus apella*) rescued from the pet trade. Five individuals that were kept in social isolation whilst they were a pet (Isolation condition) were compared to five individuals that were kept in social groups (Social condition). There was a significant difference between the frequencies of abnormal behaviours between the two housing conditions ($P = 0.008$). Individuals in the Isolation condition performed more abnormal behaviours than the individuals in the Social condition. There was also a significant difference in the frequencies of feeding (including foraging) behaviours ($P = 0.032$), with the Social condition showing much higher frequencies of feeding behaviours than the Isolation condition. These results emphasise the importance of appropriate social housing for primates in the pet trade, as years of social rehabilitation have evidently not abolished these abnormal behaviours that originated from being kept in social isolation as pets. Furthermore, it reiterates that primates are not suitable pets as most environments cannot suitably meet their complex ethological and social needs.

Introduction

Despite the fact that it is widely accepted that non-human primates (hereafter referred to as primates) are not suitable animals to be kept as domestic pets (Schupplit and Fraser, 2000; Soulsbury et al., 2009), the exotic pet trade in the UK sees thousands of privately owned primates being kept in inadequate physical and social environments (Aldrich and Hevesi, 2010). It is currently legal to keep most species of primates as pets in the UK with the appropriate licence from the pet owner's local council, with certain species not even requiring a license to be kept (The Dangerous Wild Animals Act, 2007). There are no exact figures available to determine how many primates there are in the UK pet trade (Soulsbury et al., 2009), not only because not all of them require licences, but also because it is estimated that there is wide-spread non-compliance with obtaining and owning licences for pet primates (Greenwood et al., 2001). Aldrich and Hevesi (2010) estimate this to be around 82-95%.

There is also minimal legislation and regulation to protect these primates and ensure that their needs are being met whilst being kept as a pet. DEFRA (2009) released a Code of Practice for the Welfare of Privately Kept Non-Human Primates, guiding pet owners on how to care for their pet primates, as each different species have very specific and complex dietary, environmental and social requirements (Schupplit and Fraser, 2000; Soulsbury et al., 2009). However, as these are guidelines are unenforced they are often not followed by pet owners, and so knowledge of the appropriate requirements for keeping primates as pets are not efficiently utilised, and thus essential needs are not met (Soulsbury et al., 2009).

One of a primates most fundamental needs, when being kept in captivity, is being housed in the appropriate social setting (Boere, 2001; DEFRA, 2009), and for the majority of primate species this means a social group (DEFRA, 2009). However, in the UK pet trade, it is very common for primates to be kept alone; the RSPCA (RSPCA and Wild Futures, 2012) reported that in 61% of the cases where they rescued a pet primate, the primate had been housed alone.

A social environment is essential for vital learning opportunities and for both cognitive and behavioural development in primates (Boere, 2001); therefore, social deprivation or isolation can cause significant detrimental outcomes to both physical and psychological health (Cacioppo et al., 2011; DEFRA, 2009; Gluck et al., 1973; Harlow et al., 1965; Lewis et al., 2000). Social deprivation is a major source of stress for captive primates as it inhibits species-typical behaviours (Morgan and Tromborg, 2007). Primates reared in total social isolation for the first few months of their life exhibit unnatural and abnormal behaviours including self-mutilation, inadequate social interactions, and stereotypical repetitive movements (Harlow et al., 1965). Further and prolonged social isolation has even more significant and long-lasting behavioural and social effects on primates (Harlow et al., 1965). It can almost obliterate their ability to interact appropriately in most social situations, even after being integrated into social groups. Multiple behavioural, physical and social issues including over-aggression, self-aversive behaviours, repetitive movements, abnormal sexual behaviours, depression, and in some severe situations death, occur as a result of poor social housing (Boere, 2001; Cacioppo et al., 2011; Gluck et al., 1973; Harlow et al., 1965; Lewis et al., 2000).

There is evidence to show, however, that the effects of total social isolation can be ameliorated, although this is very dependent on multiple factors, including the amount

of time the individual spent in isolation, the amount of time the individual spent in social rehabilitation, but also the rehabilitation process itself (Arling and Harlow, 1967; Harlow et al., 1965; Suomi and Harlow, 1972). Some studies even suggest that there is no critical period for primates to learn social behaviours and affiliations, and that it is possible for primates to learn social behaviours following isolation and to experience a reduction in certain abnormal behaviours with the correct social rehabilitation (Novak and Harlow, 1975; Suomi and Harlow, 1972).

There are differences, however, between the social and physical environments of captive primates in zoological or laboratory settings, and privately kept primates in the pet trade. Thus, studies that analyse the effects of abnormal social environments on primate behaviour and physiology in zoological or laboratory settings may not fully reflect all aspects of the trade when applied to pet primates, including the drastic variations between individuals in their experiences as pets in the trade. Another element of captivity that is not often considered is the primate's relationship with its owner, and if kept in social isolation to other conspecifics, how this relationship affects understanding of social interactions and behaviours, especially upon rehabilitation with other conspecifics, and in an environment where human presence is still prevalent. Constant or varied human presence to captive primates can significantly alter their environment and thus their behavioural and physiological responses (Morgan and Tromborg, 2007), including increased activity levels in relation to the activity of visitors (Chamove, 1988; Hosey and Druck, 1987), increased aggressive behaviours (Morgan and Tromborg, 2007), diminished positive social behaviours such as playing and grooming (Wood, 1998), and increased cortisol levels in relation to increased visitor numbers (Davis et al., 2005).

There are very few studies that assess the effects of either long-term (i.e. more than one year) social deprivation, or how they are still behaviourally and physiologically affected after many years, and even fewer that assess both aspects in combination. Kalcher et al. (2008) and Reimers et al. (2007), both observed the long-term effects of prolonged social isolation (decades in some cases) after a period of socialisation in chimpanzees (*Pan troglodytes*) rescued from laboratories. They found that the detrimental effects of social deprivation were still prevalent in adulthood, however, neither study assessed whether or not these effects were ameliorated after a long period of social rehabilitation, and this needs to be understood for the welfare of captive primates.

This study will focus on black-capped capuchins (*Sapajus apella*) rescued from the primate pet trade, that are now housed at Wild Futures' The Monkey Sanctuary. The Monkey Sanctuary offers a life-long home to rescued primates and aims to improve their physical and psychological well-being by socialising the primates into stable groups, and providing them with the correct diet and an enriched environment. A comparison of two groups of black-capped capuchins will be conducted, one group having been kept in social isolation as pets, and the other group having been housed socially, with both groups having now been socialised into stable social groups. This study aims to assess the behavioural effects of social deprivation on black-capped capuchins rescued from the primate pet trade, to understand the importance of social learning and interactions to captive primates. The objectives of this study are to observe and compare the differences in behaviour and social interactions between capuchins that were kept in social isolation and capuchins that were housed in social

groups, by assessing any variations in the expression of associated abnormal behaviours, individual time budgets and social interactions.

Methods

Ethical statement

Before any observations were conducted on the capuchins at the Monkey Sanctuary, an Animal Ethics Proposal and Off-Site Risk Assessment were submitted to the Plymouth University Animal Ethics Committee for approval. As this study only involved the observation of animals in their normal environment with no interactions or manipulations, no further ethical approvals or considerations were required.

Subjects

Ten black-capped capuchins (*Sapajus apella*) were observed in total; five had been housed in social isolation prior to arrival at the Monkey Sanctuary (Condition 1: Isolation), and five had been housed in social groups prior to arrival at the Monkey Sanctuary (Condition 2: Social). All of the individuals studied were housed in three different groups during the course of this study (See Table 1), as they were socialised into compatible groups at the Monkey Sanctuary and were not grouped according to their previous housing condition.

Table 1: Subject profiles. Note – all ages are estimations determined by primate keepers at the Monkey Sanctuary based on physical traits and any relevant information provided by the pet owner.

Individual	Condition	Sex	Age (years)	Group name	Group size	Time as a pet (years)	Time in isolation (years)	Time at the Monkey Sanctuary (years)
Billy	Isolation	M	7	FROSTY	7	3	3	4
Boo	Isolation	F	14	FROSTY	7	6	6	8
Charlie Brown	Isolation	M	16	FROSTY	7	5	4	11
Joey	Isolation	M	18	KODAK	4	9	9	9
Kodak	Isolation	M	13	KODAK	4	5	5	8
Banjo	Social	M	7	ELVIS	6	4	N/A	4
Betty	Social	F	20	ELVIS	6	4	N/A	4
Elvis	Social	M	20	ELVIS	6	4	N/A	4
Kirsty	Social	F	20	KODAK	4	11	N/A	5
Sue	Social	F	20	FROSTY	6	4	N/A	4

Four of the individuals in the Social condition (Elvis, Sue, Betty and Banjo) were housed together prior to arrival at the Monkey Sanctuary and were kept together as a stable group following their rescue. Banjo is the offspring of Elvis and Sue, and the two other members of their group (that were not focal individuals in this study) were both fathered by Elvis, one with Betty and another with Sue. There were two more individuals in this group when they were rescued, but both passed away. The final subject in the Social condition, Kirsty, was kept by two different pet owners, both times with another capuchin. Despite being rescued alongside one of these capuchins, they were later split into separate groups at the Monkey Sanctuary. Kirsty was eventually

socialised into the KODAK group with Joey and Kodak, and a few years later another male (not a focal individual in this study) joined their group.

As all the individuals in the Isolation condition were housed alone as pets, they were socialised into compatible groups following their rescue. Charlie Brown was housed in isolation until a year before he was rescued, and was kept with this individual upon arrival at the Monkey Sanctuary; however, she passed away not long after they arrived. After spending time socialising with multiple other capuchins, Charlie Brown was eventually integrated into the FROSTY group (containing four other capuchins that were not focal individuals in this study). Boo Boo and Billy were also both socialised into the FROSTY group. Kodak and Joey both spent a while socialising with a few different capuchins before eventually settling into the KODAK group.

Housing and routine

All six groups of capuchins at the Monkey Sanctuary undergo a move every few weeks to allow them to experience a change in enclosures for enrichment purposes. Outdoor spaces were composed of ropes, beams, shelves, trees and natural foliage; indoor spaces were heated (at approximately 20°C) and were composed of ropes, beams, shelves and bunks. The size and amount of each enclosure aspect varies between enclosures, there were also long-term and short-term enrichment items placed in all enclosures. There were multiple runways and hatches connecting all the enclosures allowing easy movement between spaces.

Enclosures were cleaned by staff and volunteers every morning, and during this period the groups were temporarily moved out of each space. New enrichment items were put into the enclosures, and each group's morning feed was spread around. Once all of the enclosures were cleaned, each group was given a scatter of sunflower seeds (at around 11am). At around 2pm each group was given a second scatter of either nuts, fruit, mealworms or various carbohydrate items including rice cakes or pasta. Finally, at around 4pm, each group was given their afternoon feed. Morning and afternoon feeds consisted of vegetables, nuts, lentils, beans and pulses; porridge (that contained vitamin supplements – multi-vitamins, folic acid, glucosamine, joint omega oil and ester C) was also provided in the morning feeds only.

Data collection

Each of the three groups (KODAK, ELVIS and FROSTY), containing the ten focal subjects, were observed for a two day period; the KODAK group were observed on 01.10.16 and 02.10.16, the FROSTY group were observed on 08.10.16 and 09.10.16, and the ELVIS group were observed on 15.10.16 and 16.10.16. Each group were in different enclosures during their observation periods, and the amount of space provided was relative to the overall group size. The KODAK group were in the enclosure 'Paddock' (approximately 120m²) which contained the 'Paddock hut' (see Figure 1). The FROSTY group were in the enclosures 'Dell' (approximately 58m²) which contained the 'Dell Hut', 'Room 6' (approximately 15m²), 'Veg Patch' (approximately 18m²) and 'Room 5' (approximately 15m²) (see Figure 1). The ELVIS group were in the enclosures 'Web' (approximately 90m²), 'Orchard Hut' (approximately 12m²), 'Orchard (including Partition)' (approximately 18m²) and 'Room 4' (approximately 24m²) (see Figure 1).

The Monkey Sanctuary was open to the public throughout each of the recording periods for all groups meaning that visitors were present on site; however, the visibility

of the visitors to each group varied slightly depending on the locations of each group's enclosures (see Figure 1).



Figure 1: An aerial view of the enclosures in the capuchin territory at the Monkey Sanctuary (not to scale). Abbreviations; O.Hut = Orchard Hut, Part. = Partition, R4 = Room 4, R5 = Room 5, R6 = Room 6, D.Hut = Dell Hut and P.Hut = Paddock Hut. Original picture provided by the Monkey Sanctuary.

Using instantaneous scan sampling, behaviours (see Table 2) were recorded by an observer at 30 second intervals during a 30-minute period, five times a day. Each observation period was also recorded using a Canon Legria HF R47 video camera, and the footage was watched later to ensure that observed behaviours were recorded reliably.

Behavioural definitions were adapted from an ethogram provided by the Monkey Sanctuary and through personal observations, and abnormal behaviours were defined through personal observation and then approved by the Monkey Sanctuary.

Table 2: The ethogram used to determine behaviours during observations; behaviours classified as abnormal are highlighted in bold, social behaviours are underlined. These behaviours are not all mutually exclusive, therefore may be recorded at the same time (e.g. 'eat' and 'rest').

BEHAVIOUR:	DESCRIPTION:
Walk	Locomotion at a normal pace on the ground or on ropes, beams, platforms and any other furnishing
Run	Locomotion at a fast pace on the ground or on ropes, beams, platforms and any other furnishing
Climb	Ascending or descending on beams, ropes, mesh and any other furnishings
Eat	Consuming food, this includes mastication but also holding and examining food items
Forage	Exploring the ground or enrichment object with hands and/or mouth
Rest	Individual is motionless, this includes sitting, lying down and sleep
<u>Dominance</u>	Performing threatening behaviours in order to gain access to desired resources e.g. baring of teeth, chasing or moving another individual away
<u>Submission</u>	Performing behaviours to alleviate tension from aggressive or dominant situations or individuals e.g. fear grin, looking or moving away
Self-mutilation	Purposefully harming themselves e.g. chewing on or biting at digits or tail, fur plucking; or re-opening wounds e.g. picking at scabs or cuts
Self-grasp	Individual grabs at own body or limbs, either holding still or mock playing with them
Hand-wringing	Individual rubs hands together in small circular motions
Rocking	Repetitive movement of the entire body in a backwards and forwards or side to side motion
Spin	Entire body pivoting in a tight or small circle
Head-twist	Spinning head around in small motions from front to side, or side to side
Somersault	An entire body flip, on the ground or in the air, from back to front, front to back or side to side
Finger-sucking	Putting digits in the mouth and sucking
Bar-biting/tongue-playing	Licking, sucking or biting mesh or other furnishings

Tail wagging	Quick movements of the tail in a up and down or side to side motion
<u>Solicit</u>	Attempting to gain the attention of another individual in order to mate with them, includes eyebrow raising, following the individual, pulling their fur or hitting them and then moving away
<u>Mating</u>	Sexual intercourse, includes mounting
<u>Groom</u>	Picking through the fur, skin or teeth of another individual with hands or mouth, classified as a positive social behaviour
<u>Being groomed</u>	Another individual picking through their fur, skin or teeth with hands or mouth, classified as a positive social behaviour
Self-grooming	Picking through own fur, skin or teeth with hands or mouth
<u>Play</u>	Engaging in play behaviours with other individuals, classified as a positive social behaviour
<u>Aggression</u>	Either towards other individuals or in defence, e.g. chasing, fighting, biting, classified as a negative social behaviour
Aggression towards visitors	Towards members of the public or in defence, e.g. shaking the mesh, screaming
Aggression towards staff	Towards members of staff or in defence, e.g. shaking the mesh, screaming
Watching visitors	Observing members of the public, following their movement with eyes and/or body, includes interactions e.g. visitors attempting to engage with individuals through sound or movement
Watching staff	Observing members of staff, following their movement with eyes and/or body, excludes any interactions
Out of sight	Individual is not visible
Other	Any behaviour not previously listed

Certain behaviours can only be classified as abnormal in analysis, for instance excessive walking (comparative to other individuals) can later be classified as pacing, but recorded as 'walking' during observation; similarly, excessive grooming (comparative to other individuals) can later be classified as over-grooming, but recorded as 'grooming' during observation.

Analysis

The behaviours were grouped into ten final categories (see Table 3) for analysis. Certain behaviours were not used in analysis as they were either irrelevant to the outcome ('out of sight') or not observed during the study ('somersault' and 'other').

Table 3: Final behavioural categories used for analysis

CATEGORY	RELEVANT BEHAVIOURS
Locomotion	Walk, Run, Climb
Feeding	Eat, Forage
Rest	Rest
Dominance	Dominance
Submission	Submission
Abnormal	Self-mutilation, Self-grasp, Hand-wringing, Rocking, Spin, Head-twist, Somersault, Finger-sucking, Bar-biting/tongue-playing, Tail wagging, Watching Visitors, Watching Staff
Sexual	Solicit, Mating
Grooming	Groom, Being groomed, Self-grooming
Play	Play
Aggression	Aggression, Aggression towards visitors, Aggression towards staff

The data was collated in Microsoft Office Excel (2007) before being analysed in IBM SPSS Statistics 23.0. Mann-Whitney U tests were conducted to assess the differences between the two conditions, 'Isolation' and 'Social', in the frequencies of the behaviours that were performed. During the observation period for the ELVIS group, one of the females (Betty) in the Social condition was in oestrus, meaning that her behavioural repertoire was drastically different to that of a capuchin that is not in oestrus (Carosi et al., 1999). This individual was therefore removed from the data, and the Mann-Whitney U tests were repeated to assess differences between the two conditions in the frequencies of behaviours that were performed without this individual.

Results

Comparison of behavioural frequencies between conditions

Individuals in the Social condition showed significantly fewer 'abnormal' behaviours than the individuals in the Isolation condition ($U=0$, $P = 0.008$; without Betty $U=0$, $P = 0.016$ – see Figure 2).

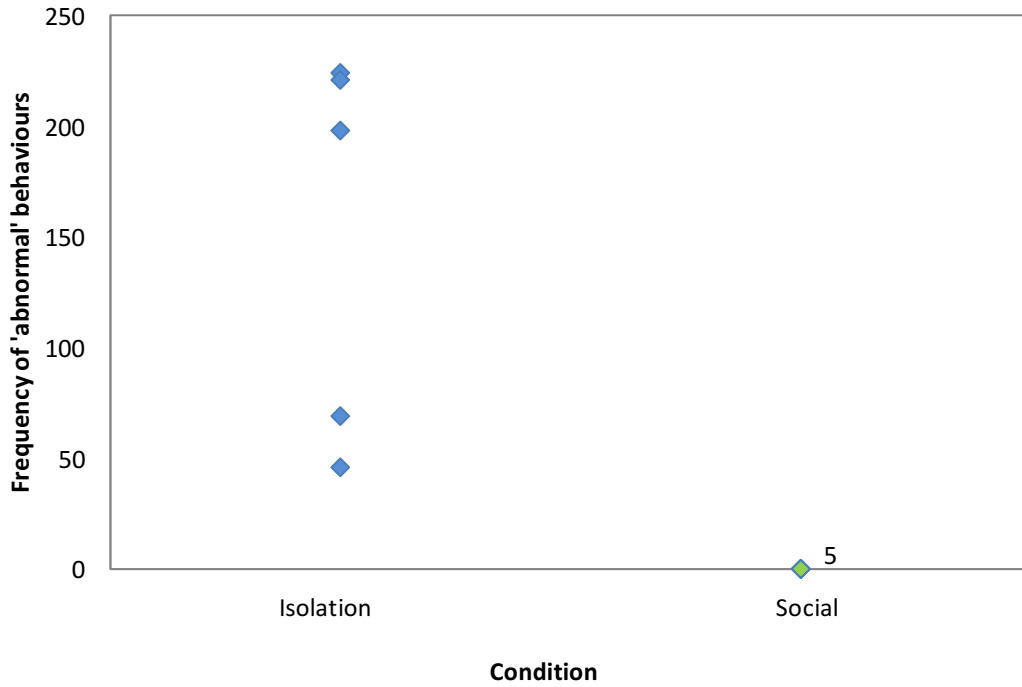


Figure 2: The frequency of 'abnormal' behaviours shown by each condition. Y axes across Figures 2-11 may differ due to variations in frequencies between behaviours. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary. Frequencies produced by multiple individuals are marked in green; the amount of individuals is labelled adjacent each point.

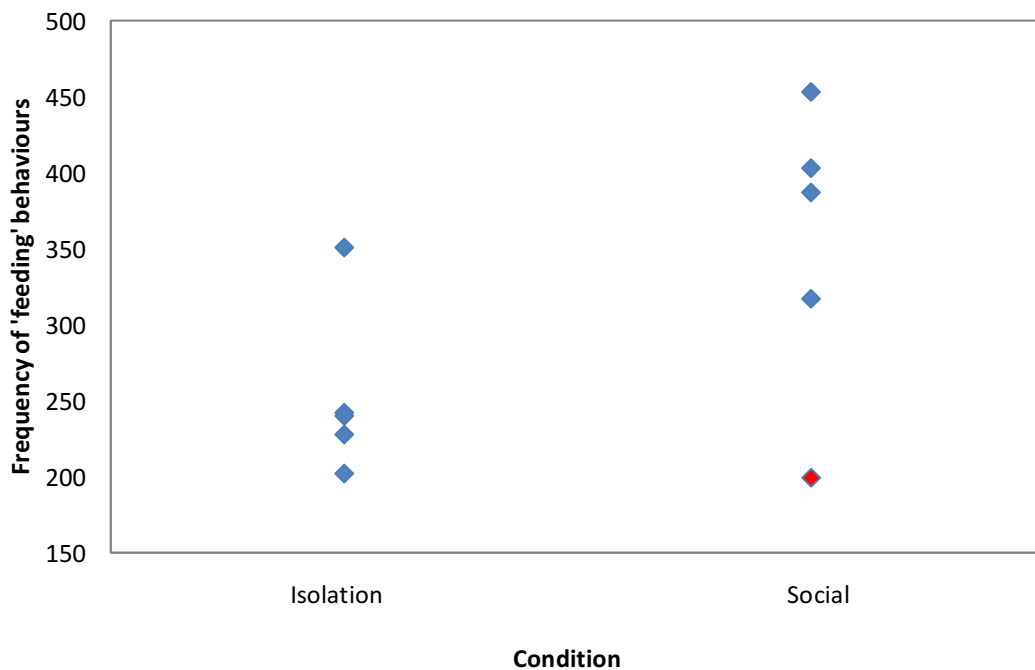


Figure 3: The frequency of 'feeding' behaviours shown by each condition; the individual in oestrus (Betty) is marked in red. Y axes across Figures 2-11 may differ due to variations in frequencies between behaviours. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary.

The removal of the individual in oestrus (Betty) meant that the behaviour 'feeding' also became statistically significant between the two conditions ($U=19$, $P = 0.032$; see Figure 3), but it was not significant when she was included in the data set ($U=19$, $P = 0.222$; see Figure 3).

Although no other behaviours were statistically significant, there were noticeable differences in the frequencies of the positive social behaviour 'play' ($U=4$, $P = 0.095$; without Betty $U=3.5$, $P = 0.111$; see Figure 4), the positive social behaviour 'grooming' ($U=17.5$, $P = 0.310$; without Betty $U=17.5$, $P = 0.063$; see Figure 5) and the negative social behaviour 'aggression' ($U=3.5$, $P = 0.056$; without Betty $U=3.5$, $P = 0.111$; see Figure 6).

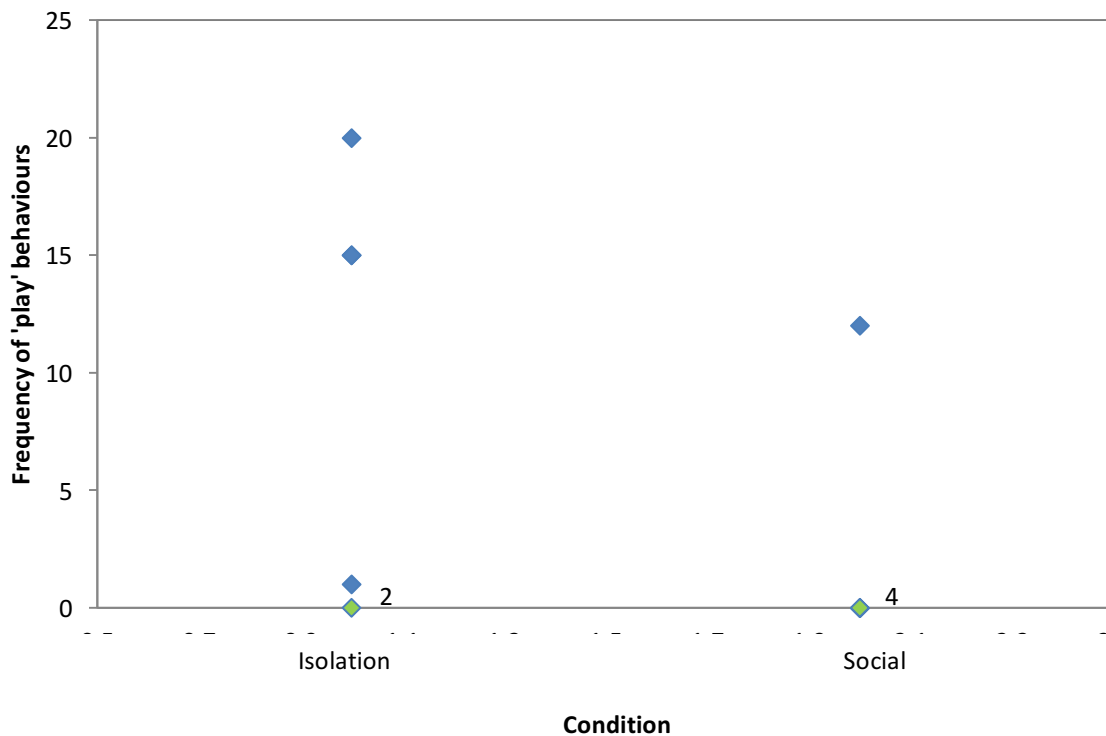


Figure 4: Frequency of 'play' behaviours shown by each condition. Y axes across Figures 2-11 may differ due to variations in frequencies between behaviours. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary. Frequencies produced by multiple individuals are marked in green; the amount of individuals is labelled adjacent to each point.

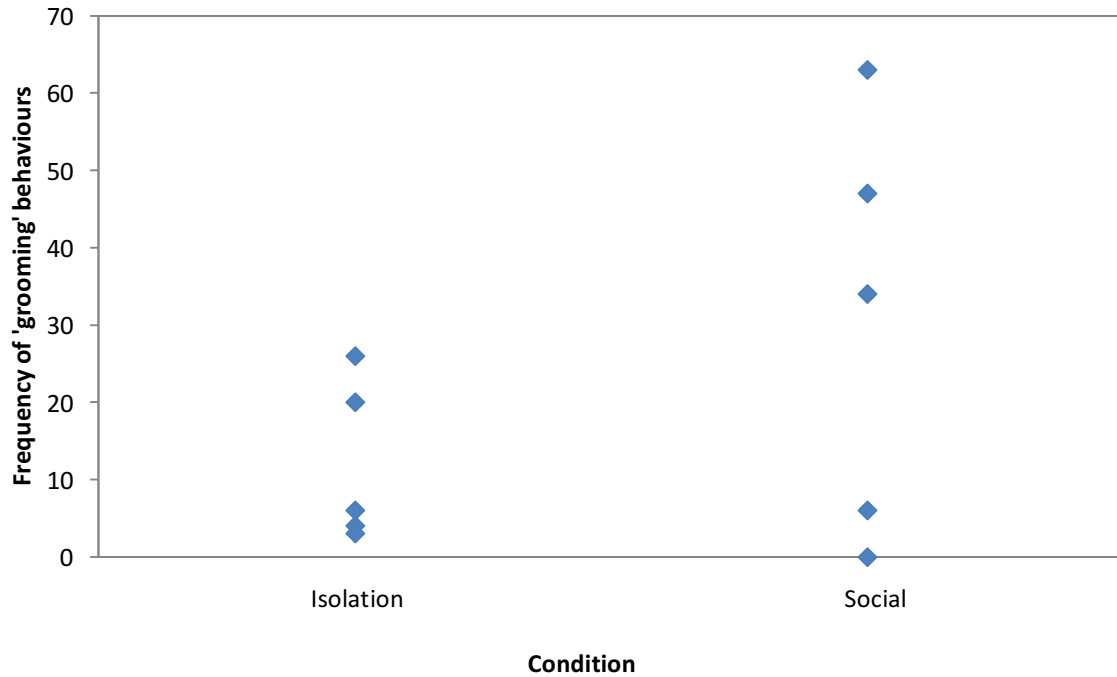


Figure 5: Frequency of 'grooming' behaviours shown by each condition. Y axes across Figures 2-11 may differ due to variations in frequencies between behaviours. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary.

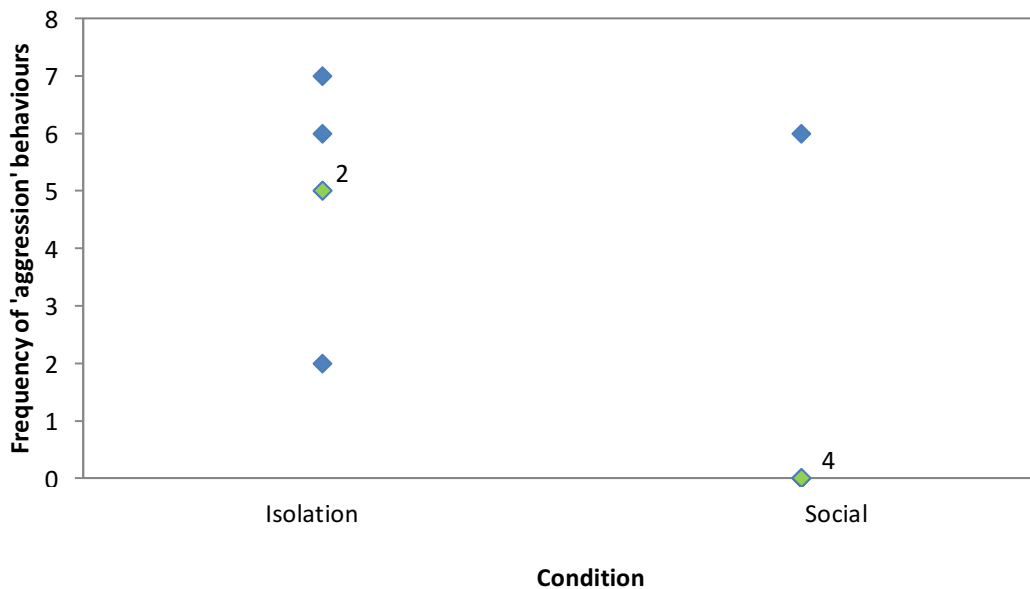


Figure 6: Frequency of 'aggression' behaviours in each condition. Y axes across Figures 2-11 may differ due to variations in frequencies between behaviours. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary. Frequencies produced by multiple individuals are marked in green; the amount of individuals is labelled adjacent to each point.

Although there was no significant difference in the performance of 'Sexual' behaviours between the two conditions ($U=10.5$, $P = 0.690$; without Betty $U=6$, $P = 0.413$; see Figure 7), it is worth noting the majority of this behaviour in the Isolation condition came from the individual Kodak, and all of his 'sexual' behaviours were with another male in his housing group that was not a part of this study.

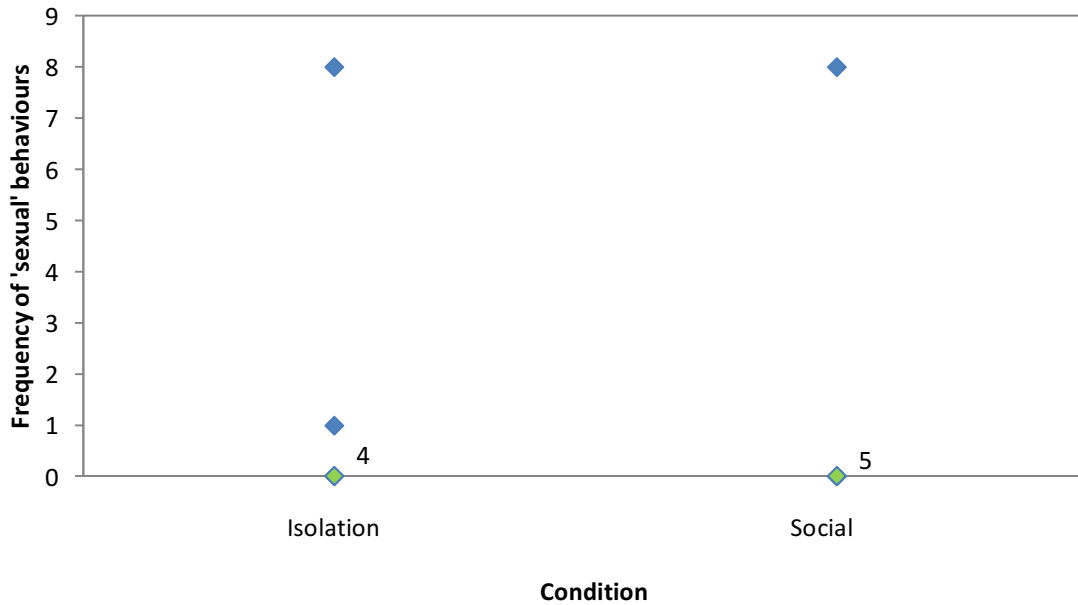


Figure 7: Frequency of 'sexual' behaviours shown by each condition. Y axes across Figures 2-11 may differ due to variations in frequencies between behaviours. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary. Frequencies produced by multiple individuals are marked in green; the amount of individuals is labelled adjacent to each point.

Though there were some noticeable differences between individuals for the performance of certain behaviours, such as 'locomotion' (see Section 3.2), as a group there was no significant difference between the two conditions; 'locomotion' ($U=13$, $P = 1.000$; without Betty $U=8$, $P = 0.730$; see Figure 8), 'rest' ($U=15$, $P = 0.690$; without Betty $U=13$, $P = 0.556$; see Figure 9), 'dominance' ($U=10$, $P = 0.690$; without Betty $U=8$, $P = 0.730$; see Figure 10), 'submission' ($U=7.5$, $P = 0.310$; without Betty $U=6$, $P = 0.431$; see Figure 11).

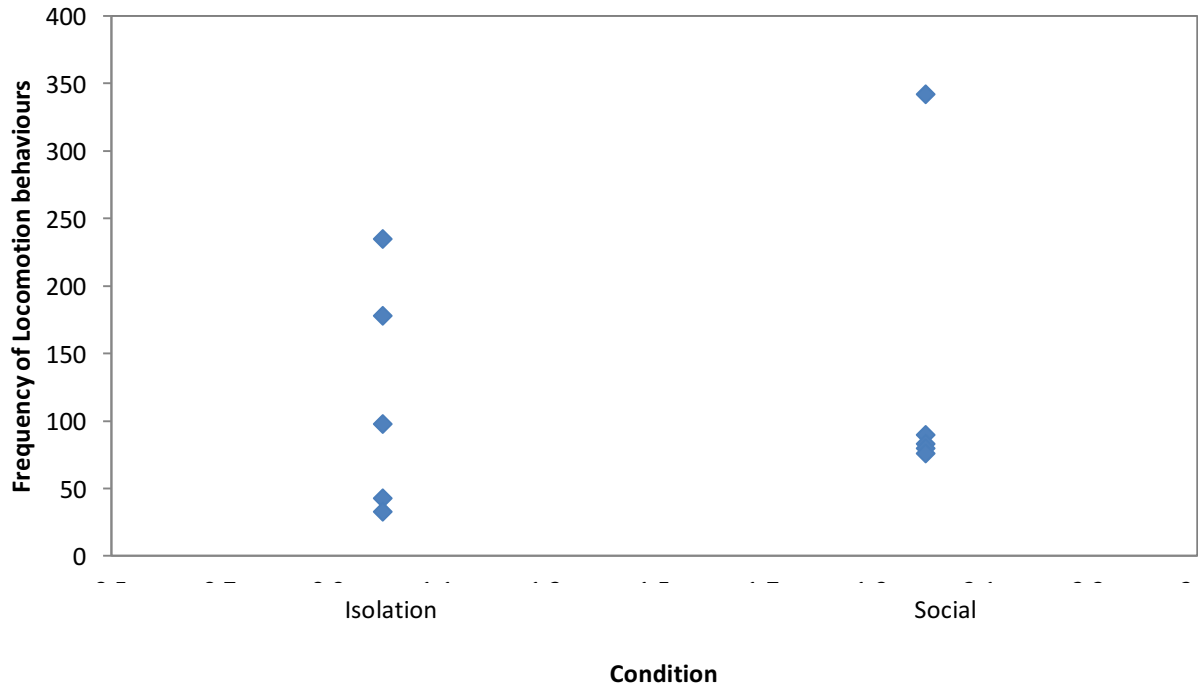


Figure 8: Frequency of 'locomotion' behaviours shown by each condition. Y axes across Figures 2-11 may differ due to variations in frequencies between behaviours. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary.

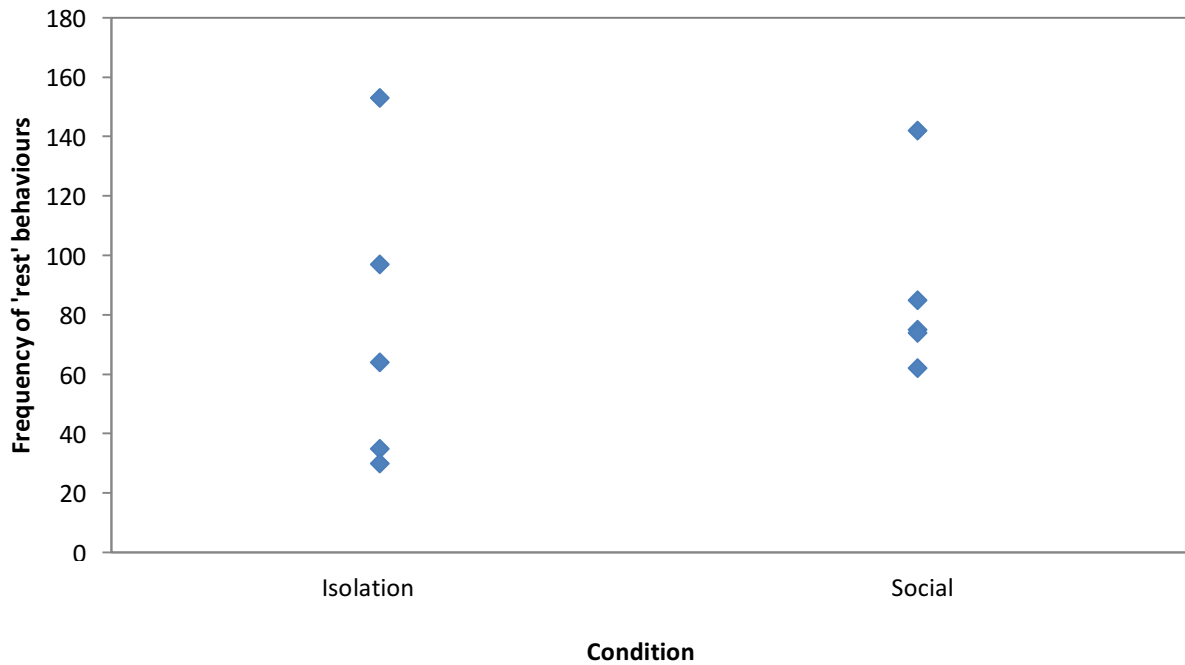


Figure 7: Frequency of 'rest' behaviours shown by each condition. Y axes across Figures 2-11 may differ due to variations in frequencies between behaviours. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary.

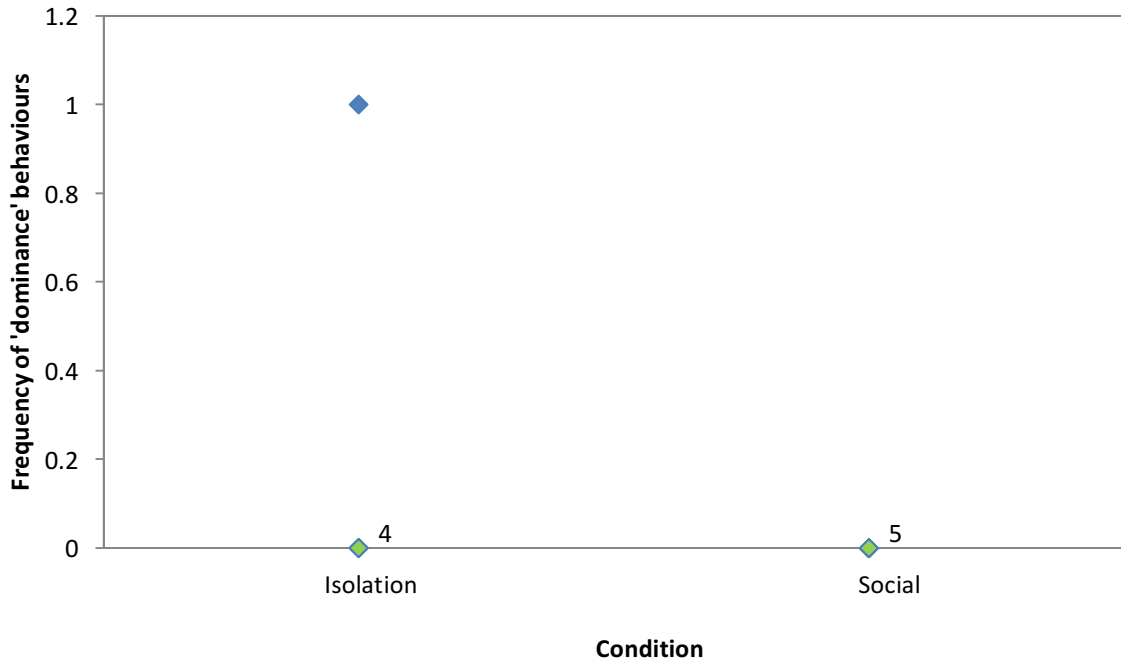


Figure 8: Frequency of 'dominance' behaviours shown by each condition. Y axes across Figures 2-11 may differ due to variations in frequencies between behaviours. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary. Frequencies produced by multiple individuals are marked in green; the amount of individuals is labelled adjacent to each point.

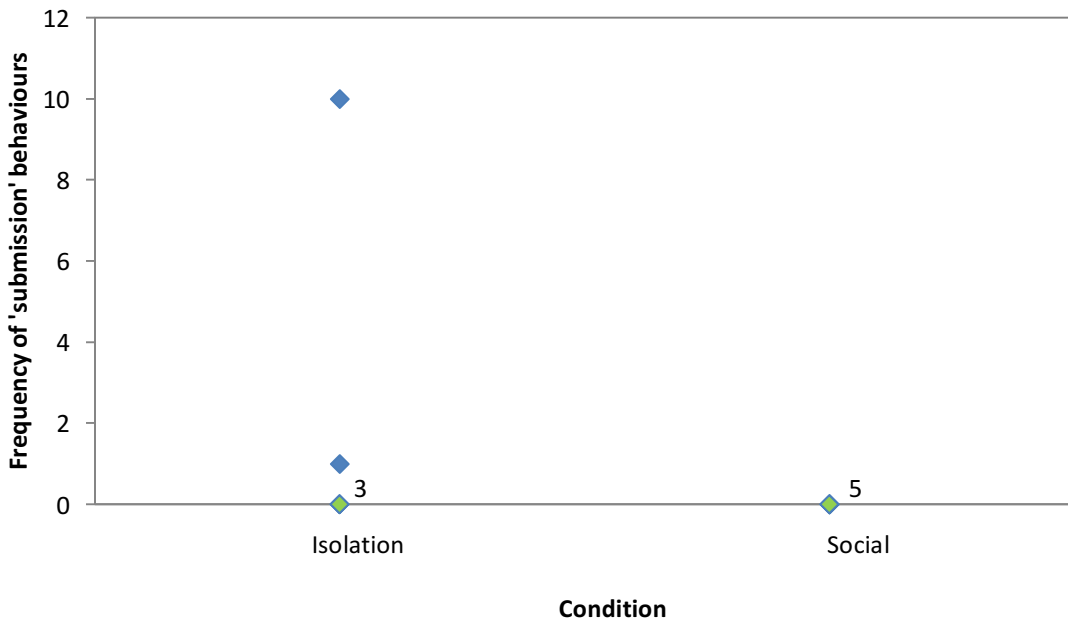


Figure 9: Frequency of 'submission' behaviours shown by each condition. Y axes across Figures 2-11 may differ due to variations in frequencies between behaviours. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary. Frequencies produced by multiple individuals are marked in green; the amount of individuals is labelled adjacent to each point.

Exploratory investigation into individual behavioural time budgets

Due to the substantial variations in behavioural frequencies between individuals of both conditions, an exploratory investigation into their behavioural time budgets was conducted to assess differences between individuals. This will allow a more in-depth analysis based on multiple aspects such as their different histories in the pet trade and any variations in each individuals social rehabilitation process.

Key for Figures 12 and 13:

Behaviour codes:

L = Locomotion, F = Feeding, R = Rest, D = Dominance, S = Submission, A= Abnormal, X = Sexual, G = Grooming, P = Play, N = Aggression

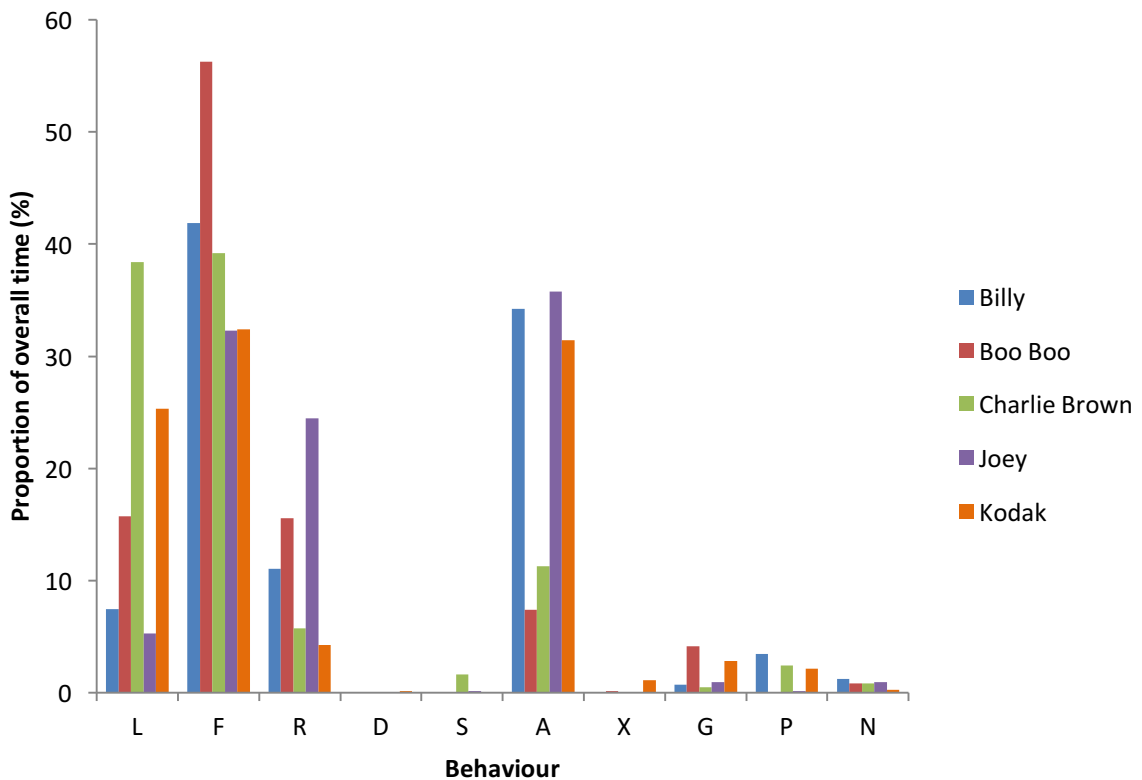


Figure 12: Behavioural time budget for individuals in the Isolation condition. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary.

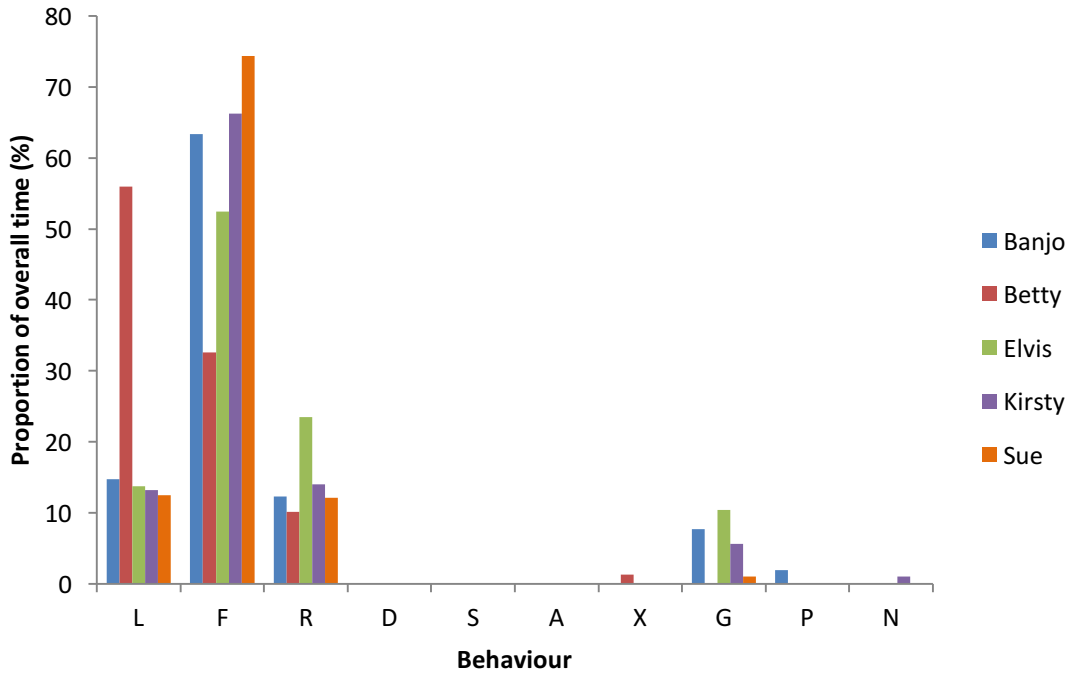


Figure 13: Behavioural time budget for individuals in the Social condition. As the behaviours observed in this study were not mutually exclusive, the total amount of behaviours shown by each individual may vary.

Discussion

Abnormal behaviours

There was a significant difference between the two conditions in the performance of abnormal behaviours, with the individuals in the Isolation condition showing much higher frequencies of abnormal behaviours than the individuals in the Social condition, even after years of social rehabilitation. This finding supports the work of Harlow et al. (1965) by showing that a period of early social deprivation in primates can cause the development of abnormal behaviours that are still present in later life. Also, that the social rehabilitation process is not always completely effective at abolishing these behaviours as it is very dependent on multiple factors regarding the amount of time each individual spent in isolation, the amount of time each individual spent in rehabilitation and the variations of the rehabilitation process itself to each individual (Arling and Harlow, 1967; Harlow et al., 1965; Suomi and Harlow, 1972), all of which were very specific to each individual in both of the conditions.

One major difference between this study and the experiments done by Harlow et al. (1965), is that these individuals experienced prolonged periods of social isolation (from 3 to 9 years) and have been in social rehabilitation for long periods of time (from 3 to 11 years). Similar studies have been conducted that assessed the effects of long-term (decades in some cases) social deprivation on chimpanzees (Kalcher et al., 2008; Reimers et al., 2007) and found the detrimental effects were still present in adulthood, however, neither assessed these effects after long periods of social rehabilitation. This study has shown that this is also the case for capuchins rescued from the pet trade. However, as there was no data available to assess the differences in abnormal (or any

other) behaviour during this study since immediate rescue, it is impossible to conclude whether or not socialisation resulted in a reduction of abnormal behaviours in these individuals.

During this study, there were no abnormal behaviours shown by any of the individuals in the Social condition. This result is very suggestive of the importance of social housing to captive primates; however, there are some factors that have to be taken into consideration when assessing this. Firstly, this study was done on a very small number of individuals, over a relatively short period of time, in one institution, and perhaps if these aspects were different (i.e. a larger number of individuals, a longer observation period, and at other institutions), different results may have been found. Furthermore, certain abnormal behaviours recorded in this study, such as 'watching visitors', may have been affected by the fact that some individuals in the Social condition (Banjo, Betty, Elvis and Sue) were a lot further away than the other individuals (and thus a lot less visible) to visitors, as this can affect the performance of stereotypical behaviours (Chamove et al., 1988). Therefore, if all individuals had been observed in the same enclosure with the same visibility and proximity to visitors, these results may have been different. Finally, it must also be taken into consideration that these same members of the Social condition (Banjo, Betty, Elvis and Sue) were all housed together prior to and post rescue, and are related. Therefore, for the other individual in the Social condition (Kirsty), and for all of the individuals in the Isolation condition, the additional stressors of group stability changes and introductions to unfamiliar individuals were an element of their rehabilitation process. The social history of the group in which an individual is socialised into can affect the rehabilitation process, and if there are no socially experienced individuals in the rehabilitation group, as is the case with Kirsty, then the process can be harder to adapt to (Kalcher et al., 2008; Suomi and Harlow, 1972).

There were also notable variations in the abnormal behaviours shown by the Isolation condition; the individuals Boo Boo and Charlie Brown spent less of their overall time performing abnormal behaviours (7.37% and 11.26% respectively), compared to the other members of the condition (between 31.45% and 35.78%). There are several possible explanations for this, one being that Charlie Brown has been in rehabilitation for the longest of all individuals in this condition (11 years), but also that they are both members of a large group (relative to some of the other individuals), containing individuals with a social history. This reiterates the findings from Kalcher et al. (2008) that being with socially experienced individuals during socialisation can aid rehabilitation.

Fundamentally, the difference between the two conditions in their performance of abnormal behaviours alludes to the importance of social housing for captive primates for the prevention of the development and perseverance of abnormal behaviours, as its effects are long-lasting and detrimental.

Feeding behaviours

With the removal of the individual in oestrus (Betty), there was a significant difference between the two conditions and their performance of feeding (including eating and foraging) behaviours, with the Isolation condition spending much less of their overall time 'feeding' (mean 40.41%) compared to the Social condition (mean 64.1% - without Betty). The effects of social deprivation on feeding behaviours are not well documented, as there is potentially little correlation between the two; however, general

aspects of captivity can be attributed to this difference, such as the presence of large numbers of visitors causing a reduction in foraging behaviours (Wood, 1998). As all members of the Isolation condition were much closer and visible to visitors than most members of the Social condition (Kirsty being the exception), this is a possible explanation.

There are other possible reasons for this difference however, as certain abnormal behaviours, such as rocking, were not often performed at the same time as other behaviours such as eating or foraging. Therefore, as individuals in the Isolation condition spent a larger proportion of their time performing abnormal behaviours, they had less time available for behaviours such as feeding. DEFRA (2009) state that foraging is a large and important part of a captive primate's daily behavioural time budget, and therefore a significant reduction in feeding behaviours due to previous housing conditions, does suggest that the housing was inadequate, but whether or not this developed due to an abnormal social environment or an inappropriate physical environment, is not always possible to assess (Ridley and Baker, 1982).

Play behaviours

There were notable, but not significant, differences between the two conditions in their performance of play behaviours, with the Isolation condition showing more play behaviours than the Social condition. This supports the findings of Suomi and Harlow (1972) that the rehabilitation process encourages the performance of play behaviours, therefore, as the individuals in the Social condition did not experience a social rehabilitation, this would not have affected them. The mean age of the Isolation condition is lower than that of the Social condition (13.6 and 17.4 respectively), suggesting that individuals in the Isolation condition are more likely to play due to being younger, additionally the only individual in the Social condition to play was their youngest member, Banjo (7 years of age). Overall, the frequencies of play behaviours across both conditions were very low; therefore, it is difficult to make definitive conclusions without more data.

Grooming behaviours

The Social condition performed more grooming behaviours than the Isolation condition; however, it was not a significant difference. The fact that grooming, a positive social behaviour, is present within the Isolation condition supports the conclusions made by Novak and Harlow (1975) and Suomi and Harlow (1972) that it is possible for individuals to learn social behaviours following a period of social isolation. However, the fact that it was seen less in the Isolation condition could be due to the fact that early social deprivation leads to lower levels of positive social behaviours in adulthood, when compared with individuals that did not experience early social deprivation (Kalcher et al., 2008; Reimers et al., 2007). As with some of the other behaviours, visitor presence can also reduce levels of grooming shown by individuals (Wood, 1998). Overall, however, the frequencies of grooming in this study were very low, so again it is hard to draw definitive conclusions.

Aggression behaviours

There was a notable, but not significant, difference between the two conditions in their performance of aggressive behaviours, with the Isolation condition displaying more than the Social condition. This is in line with the findings of Suomi and Harlow (1972) that individuals deprived of social interaction show excessive aggressive behaviours later in life due to an inability to learn appropriate social interactions. Similarly to the

other social behaviours already discussed (play and grooming), levels of aggression can also be affected by visitor presence. Wood (1998) showed that high levels of visitors can increase displays of aggression within chimpanzees, so perhaps this explains the slightly higher levels of aggression shown by the individuals in the Isolation condition, but also the one member of the social condition, Kirsty, that was also in the enclosure that was in the closest proximity to the visitors. Kirsty is also the only member of the Social condition in a group with individuals of socially deprived backgrounds, and thus may have been aggressive towards them if they were acting inappropriately towards her, because, as mentioned before, they are less likely to have learnt how to interact appropriately in certain social situations (Suomi and Harlow, 1972). However, the overall frequencies of aggressive behaviours shown across both conditions were very low, so it is difficult to come to any decisive conclusions without more data.

Sexual behaviours

There was no significant difference in the performances of Sexual behaviours between the two conditions, however, the majority of the sexual behaviours in the Isolation condition were displayed by the individual Kodak, who was soliciting and mating with another male (this individual was not observed in this study). These findings are similar to that of those by Harlow et al. (1965) who found homosexual behaviours were more common in captive rhesus macaques (*Macaca mulatta*) that had been kept in social isolation, as they were unable to learn typical sexual interactions.

Locomotion behaviours

Though there was no significant difference in locomotion behaviours between the two conditions, the individuals within the Isolation condition showed varied amounts of time spent in locomotion. The individuals Kodak and Charlie Brown spent an interestingly large amount of their time in locomotion (25.32% and 38.40% respectively), from this it is possible to conclude that these individuals were pacing. Pacing is often a result of a poor environment (Boere, 2001); however, it is difficult to discern whether or not pacing behaviours develop due to constraints of an inadequate physical environment or a socially deprived environment (Ridley and Baker, 1982), as the two often go hand-in-hand in the primate pet trade.

The individual Betty (from the Social condition) also spent a significant amount of her overall time in locomotion (55.97%), when compared to the rest of the Social condition (mean 13.52% - without Betty); however this is most likely due to the fact that she was in oestrus during observation, thus spent a lot of her time moving around trying to solicit a mate (Carosi et al. 1999).

Rest, dominance and submission behaviours

There were no significant differences in rest behaviours between the two conditions, nor were there significant differences between the performance of dominance or submissive behaviours, however as the latter two behaviours occurred at such minute levels across all individuals, it is difficult to make any assumptions about the long-term effects of social deprivation on these individuals' behaviours.

Limitations

One of the major limitations of this study was the small number of individuals used in both conditions. Had more been available to study, more definitive conclusions regarding the long-term effects of social deprivation on rescued primates could have

been drawn from the data. Furthermore, if there had been data available from each individual's arrival at the Monkey Sanctuary, a comparison of the differences in behaviours between the two conditions would allow a stronger assessment of the effect of socialisation on the amelioration on certain behaviours derived from social deprivation. There were quite a few behaviours seen in this study that were potentially affected by the presence of visitors, and so if this had been controlled for, it would have been easier to distinguish behavioural origins thus making the discovered results slightly more reliable.

One point to consider when assessing the long-term effects of isolation on each condition as a whole is that, due to the very nature of the pet trade, each individual's experience would have been entirely different. There will be differences in the amount of time they were socially deprived for, the structure of their physical environment, and their relationships with their owners, which will all result in variations in the recovery of individuals (Hemsworth, 2003; Reimers et al., 2007; Ridley and Baker, 1982). Further studies into the long-term effects of inappropriate social environments on multiple primate species will allow a more comprehensive understanding of primate welfare in the pet trade.

Conclusions

It can be deduced from this study that social deprivation of primates in the exotic pet trade does have long-term behavioural effects. It alters their ability to interact appropriately in certain social situations, causes the development of abnormal and detrimental behaviours that persist into adulthood, and develops variations to 'normal' time budgets in individuals. However, this study also showed that social deprivation does not completely abolish the ability to learn certain social behaviours and interactions, such as grooming, if the appropriate social rehabilitation process is provided.

Ultimately, social deprivation and the subsequent recovery from it is a very individual experience. But one definitive issue that this study raises is that keeping primates as pets in incorrect physical and social environments has long-lasting and detrimental effects on their behavioural and psychological health. Therefore, the findings from this study support the argument that the primate pet trade should be banned, or if not, regulated in a far stricter manner that prizes primate welfare above all else.

Acknowledgments

I would like to thank my advisor Nikolaus von Engelhardt for his help and guidance, Jane Ackerman (and the rest of the eco-loans team) for the provision of the camera equipment used, and the Monkey Sanctuary for allowing me to observe their primates and for providing me with plenty of help and expert knowledge.

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