

Research Article

Effects of rearing on the behaviour of zoo-housed chimpanzees (*Pan troglodytes*)

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Abstract

Early-life experiences may considerably affect the behavioural patterns of adult primates. Particularly, atypical rearing practices might lead to abnormal behaviours and social-sexual deficiencies in captive, adult non-human primates. We conducted behavioural observations of mother-reared (n = 5) and hand-reared (n = 6) adult chimpanzees in a social group at Parco Natura Viva, Italy. We used continuous focal animal sampling to collect behavioural data focusing on individual and social behaviours. We found that all study subjects performed individual and social species-specific behaviours. However, mother-reared chimpanzees performed locomotion and affiliative behaviours significantly more than hand-reared subjects. In addition to these species-typical behaviours, hand-reared chimpanzees showed significantly more abnormal behaviours than mother-reared subjects. Therefore, these findings suggest that hand-rearing could have wide-reaching effects on the behavioural repertoire in adult zoo-housed chimpanzees. Hence, even if sometimes human intervention in rearing may be necessary to ensure the survival of captive infant chimpanzees, our results suggest that zoo-housed chimpanzees might benefit from minimized human-animal interactions and exposure to conspecifics throughout their development. These suggestions should be implemented in regular husbandry practices.

Summary

Early-life experiences may affect the behaviour of primates. We studied individual and social behaviours of zoo-housed mother-reared and hand-reared chimpanzees. Our findings suggest that hand-rearing could affect the sociality and behavioural repertoire in adult chimpanzees.

Introduction

The physical and psychological welfare of zoo-housed animals is crucial for both *in situ* and *ex situ* conservation efforts, as poor welfare might lead to stress, suppression of immune function and decrease of breeding success (Wingfield & Sapolsky, 2003; Morgan & Tromborg, 2007). The occurrence of species-specific and abnormal behaviours has been highlighted as a rigorous indicator of the welfare status in zoo-housed animals (*e.g.*, Bracke & Hopster, 2006; Hill & Broom, 2009; Spiezio et al., 2018). Particularly, the behavioural parameters involved in zoo-housed animal welfare's assessment are social interactions, problem-solving abilities, and the display of species-specific individual behaviours (Hosey et al., 2013), whereas abnormal behaviours can indicate a stressful situation (Davey, 2007; Hosey et al., 2013).

Wild chimpanzees spend most of their activity time seeking and processing food resources, travelling over long distances and using their cognitive abilities (*e.g.*, tool-use) to find high-quality food items and they have complex social relationships and communication (*e.g.*, Pruetz & McGrew, 2001; Nishida et al., 2010). They live in fission-fusion societies and have therefore complex social interactions and communication systems (*e.g.*, Pruetz & McGrew, 2001; Nishida et al., 2010). Captive chimpanzees can perform abnormal behaviours, which are absent or rare in wild conspecifics, ranging from self-injurious behaviours to repetitive locomotion or body movement (see Birkett & Newton-Fisher, 2011 for an extensive list).

Natural species-specific behaviours can be considered animal needs (*e.g.*, tool use in chimpanzees, explorative behaviour in primates, scent marking behaviour in carnivores) as they are highly motivated behaviours shown under natural conditions, pleasing and representing a biological necessity (Bracke & Hopster, 2006). On the contrary, abnormal behaviours (such as stereotypies) are displacement activities and might indicate that animals are trying to cope with stressful situations or are unable to perform their natural species-specific behaviours (Mason et al., 2007; Grandin, 2010). These behaviours can persist or even increase long after the situations in which they developed have waned, as they may be due to long-standing psychological and neural changes or to unvarying environmental conditions (Latham, 2005; Garner, 2006; Novak et al., 2006).

Early-life experiences might impact the behaviour of non-human primates and affect considerably the way they interact with their environment (Kagan, 1996; Fox & Henderson, 1999; Parker & Maestriperi, 2011; Freeman & Ross, 2014). Consequences of unnatural early-life experiences, such as lack of early social interactions, might lead to a wide array of effects, impacting both social and non-social domains (Saltzman & Maestriperi, 2011; Leshem & Schulkin, 2012; Cissy, Richard & Mats, 2014). Rearing animals in isolation from conspecifics can

negatively impact their behavioural repertoire, promoting abnormal behaviors such as stereotypies and altering brain development and chemistry (Würbel 2001; Garner, 2005; Latham & Mason, 2008; Zhang, 2017), with persistent effects over the lifespan (Murray, 1998; Nash et al., 1999). Hand-rearing (*i.e.*, rearing infants in a nursery environment under more or less extensive human contact; Ruppenthal, 1979) is a practice adopted in zoos to improve the survival chances of high-risk infants of endangered species (Ogden & Kasielke, 2001) or due to maternal rejection (Novak et al., 2006). However, there is growing evidence that early separation from the mother can lead to the unnatural development of her offspring and thus to the display of abnormal behaviours (reviewed by Latham & Mason, 2008). For instance, long-term increase of stereotypic behaviours, including self-directed behaviours, in zoo-housed primates deprived from their mother have been reported in rhesus macaques and chimpanzees (Champoux, et al., 1991; Fritz et al., 1992; Spijkerman et al., 1994; Bloomsmith et al., 2002). Similarly, hand-reared chimpanzees and gorillas (*Gorilla gorilla*) have been found to perform more stereotypies than mother-reared or peer-reared individuals (Marriner & Drickamer, 1994; Nash et al., 1999; Martin, 2002; 2005). In particular, hand-reared chimpanzees may show abnormal behaviours such as excessive rocking, self-clutching and self-mutilation (Harlow, et al., 1965; Fritz et al., 1992; Fritz & Howell, 1993; Nash et al., 1999; Brüne et al., 2006; Clay et al., 2015). Additionally, the human hand-rearing of captive animals can also produce further undesirable long-lasting behavioural changes, such as fearfulness, stress-responsiveness, apathy, aggressiveness, poor social interactions and lack of social competence (*e.g.*, Sanchez, et al., 2001; Ryan, et al., 2002; Kreger et al., 2004; Latham & Mason, 2008; Clay et al., 2015).

Hand-reared primates lack the opportunity of benefitting from maternal care, with subsequent potential impairment of their reproductive success (Ryan et al., 2002). In addition, several studies highlighted that maternal deprivation might compromise the repertoire of social behaviours in hand-reared non-human primates (Gold, 1992; Maestripieri & Carroll, 1998; Lonsdorf & Ross, 2012). Nevertheless, the effects of hand-rearing vary according to the rearing method adopted. For instance, total isolation rearing, according to which infants are raised in complete isolation from birth, could have more dramatic consequences on social development rather than surrogate-only and partial-isolation rearing (Bloomsmith et al., 2006; Novak & Sackett, 2006; Novak et al. 2006; Dettmer et al., 2012). In the latter case, infants are raised by surrogate conspecific mothers or reared with conspecifics from a certain development stage (Zhang, 2017). These adjusted practices seem to mitigate the effect of maternal deprivation on the performance of abnormal behaviour and to ameliorate the physiological and psychological wellbeing (Hotzel et al., 2004; O'Connell et al., 2005; Tuytens, 2005; Bloomsmith et al., 2006; Novak & Sackett, 2006; Novak et al. 2006; Dettmer et al., 2012). Moreover, Standard Nurseries

(ST) consisting of small groups of same-aged chimpanzees reared by humans without opportunities to perform species-specific behaviours can lead to disorganized attachment, deficits in attention and cooperation (van Ijzendoorn et al., 2009) and can have long-term effects, such as the development of abnormal behaviours (*e.g.*, stereotypies, self-injurious behaviours) and changes in the forebrain structure (Clay et al., 2015). On the other hand, Responsive Care Intervention that provides chimpanzees with the opportunity to perform species-typical motoric, communicative, social and emotional behavioural repertoire can help to mitigate the impact of hand rearing in this species. In turn, enhancing social cognition, emotional and communicative responses, present to a greater extent than in subjects raised under ST (Bard et al., 2014; Bard & Hopkins, 2018).

This study aimed to investigate individual and social behaviours of zoo-housed chimpanzees with atypical early history compared to mother-reared chimpanzees in order to assess the impact that humans had on the welfare of these captive animals. We tested the hypothesis that chimpanzees with atypical rearing would show qualitative and quantitative differences in individual and social behaviour compared to mother-reared conspecifics. In particular, we predicted that chimpanzees who experienced more exposure to humans would display more abnormal behaviours and less positive social interactions (*e.g.*, affiliative behaviour) than mother-reared chimpanzees living in the same social group.

Materials and Methods

Study subjects and housing

We studied a group of 11 adult chimpanzees, nine females and two males. Six of them (two males and four females) had an atypical early history, whilst the remaining chimpanzees were naturally raised by their mothers (**Table 1**).

[Insert Table 1 here]

Throughout the manuscript, chimpanzees with atypical early history will be referred as “hand-reared chimpanzees” (HR). Hand-reared chimpanzees included subjects that experienced different degree of exposure to humans during their early-life stages. The interaction with humans experienced by the study hand-reared chimpanzees was prolonged (several hours per day and sometimes also night) and did not involve mechanisms providing them with appropriate socio-emotional contexts. We adopted the Chimpanzee-Human Interaction Index (CHI_i) proposed by Freeman and Ross (2014) to provide information on the subgroup of chimpanzees with atypical early history. Based on the CHI_i, according to their first four years of life, each subject can be

categorized as “having only or primarily human exposure (CHI: 0-0.30), exposure to both chimpanzees and humans (CHI: 0.31-0.70), or primarily chimpanzee experience (CHI: 0.71-1.0)” (Freeman & Ross, 2014, p. 6) (**Table 1**). The information to calculate the CHI was gained from reports of the Authorities that confiscated the animals, zookeepers and veterinarians that raised the subjects. In particular, four of the six study chimpanzees with atypical early history were raised by humans from birth (Tommy, Camilla, Laretta and Giuditta) whereas two chimpanzees were reared in the presence of conspecifics with similar rearing histories from early-life stages before they were four years old (Mary and Davidino) (**Table 1**). After the human-rearing period in the rearing room (only human-exposure), these chimpanzees were housed in the nursery room together with juvenile chimpanzees having similar early-life histories. When in the nursery room, chimpanzees were equally exposed to conspecifics but still had full contact with humans. At the time of the study, the hand-reared chimpanzees were living together in the same group and enclosure since six years (Giuditta and Laretta) and ten years (Tommy, Davidino, Camilla and Mary) before the beginning of the study.

Throughout the manuscript, chimpanzees reared by their mothers will be referred as “mother-reared chimpanzees” (MR). The study mother-reared chimpanzees were raised by their biological mothers and were in continuous physical contact with conspecifics in the first months after birth, without any human intervention in any life stage, promoting species-typical motoric, social, emotional and communicative skills.

Housing

The enclosure was made of a 1,147 m² outdoor area and a 133 m² indoor area. The outdoor area of the enclosure was a grassy island with a small stream (drinking point where water was available *ad libitum*), bushes, artificial caves serving as shelters, trees, wooden towers connected through several ropes to allow climbing and brachiating, and two artificial termite mounds to stimulate tool use. The outdoor area was visible to the general public. The chimpanzees spent their daytime outdoors (from 9.00 am to 5.00 pm), when the zoo was open to the public, while their night-time indoors (from 5.00 pm to 9.00 am). When outdoors, chimpanzees had no access to the indoor enclosure and vice versa. After moving between outdoor and indoor areas, chimpanzees could find food items and different types of environmental enrichment devices. Main meals were provided in the afternoon in the indoor enclosure, although part of the daily amount of fruit and vegetables was scattered around in the outdoor enclosure approximately every two hours, to promote foraging and food processing activities. The chimpanzee diet was made of fresh fruit and

vegetables, whereas food items such as legumes, seeds, peanuts, nuts, honey, primate jellies and raisins were provided regularly as environmental enrichment. The hand-reared chimpanzees were gradually introduced to the mother-reared ones and at the time of the study all subjects were living together in the same enclosure from approximately four years.

Data collection

We collected behavioural data by using an ethogram deriving from previous studies (Pruetz & McGrew, 2001; Nishida et al., 2010; Freeman & Ross, 2014) integrated with observations of the study group (**Table 2**). The ethogram included four behavioural classes (individual normal and abnormal behaviours, social behaviours, not observed) covering 16 behavioural categories. For social behaviours (**Table 2**), actions both performed and received by the focal subject were recorded during the study. We collected data on duration of individual and social behaviours using a continuous focal animal sampling method (Altmann, 1974). Specifically, we recorded durations of different behavioural categories performed by each study chimpanzee (**Table 2**). The only abnormal behaviours reported in the study group were apathy and rocking. These behaviours were performed for a low amount of time and only by a small subgroup of the study subjects so that it was not possible to collect enough datapoints to analyse each category separately. Thus, apathy and rocking are both described in the ethogram but they were pulled together as one behavioural category for statistical analyses. “Out of sight” category is particularly relevant in zoo settings, as wild animals can sometimes try to hide in the presence of visitors, if they are perceived as negative stimuli or stressors. Thus, we decided to include the behavioural category “not observed” (including the time chimpanzees spent hiding in caves, bushes or far from the visitors’ path) in the data analysis.

[Insert Table 2 here]

We carried out 44 10-minute sessions per individual over a month period. Particularly, we conducted two daily observational sessions between 10 am and 12 pm and between 2 and 4 pm by a single observer (C.V.). The observer was blind to the goal of the study and was not informed about the rearing history of the study subjects during the data collection period. We collected behavioural data through the live observation of the study subjects, recording durations of each behavioural category using a digital stopwatch. C.V. observed the chimpanzees for three weeks before the beginning of the data collection in order to i) establish the behavioural ethogram and familiarize with the study group behaviour, and ii) allow the study subjects to get habituated to the observer presence in the visitor path. Subjects were observed in a prescribed sequence

following a specific design to avoid time-of-day bias in data collection. In particular, over the study sessions, each chimpanzee was observed in all time-lapses between 10 am and 12 pm and between 2 and 4 pm.

Data analysis

Statistical analyses were performed using non-parametric statistical tests. For each subject, we calculated durations of behavioural classes and categories per session. Within each group, the datasets used in the analyses were made of the mean duration of each behavioural category (or group of behaviours in the case of inactivity and activity) calculated for all subjects for each day of data collection (N = 22) (Regaiolli et al., 2018). The two datasets were compared between the two groups using non-parametric statistical tests. In particular, Mann-Whitney test was used to compare durations of behavioural classes and behavioural categories performed by hand-reared and mother-reared chimpanzees. Significance level was set at $P < 0.05$ and all tests were two tailed. We analysed data using StatView version 5.0 (SAS Institute Inc.). In the *Results section* are reported medians, interquartile range (IQR) and durations expressed in seconds (s).

Results

Overall time-budgets

When investigating the amount of time that the study chimpanzees (9 females, 2 males) as a group spent in different behaviours (**Figure 1**) the most performed behavioural category was visual exploration (mean = 5505.3; SD = 1814.3 s), followed by individual resting (mean = 4699.8; SD = 3414.0 s), feeding (mean = 2350.7; SD = 822.6 s), locomotion (mean = 2290.6; SD = 740.9 s), social resting (mean = 2231.4; SD = 1491.0), affiliative behaviour (act) (mean = 1773.1; SD = 1247.9 s), not observed (mean = 1643.2; SD = 1772.9 s), individual play (mean = 1640.1; SD = 1514.5 s), affiliative behaviour (R) (mean = 1405.6; SD = 656.7 s), self-directed behaviour (mean = 957.2; SD = 1256.0 s), agonistic behaviour (R) (mean = 767.9; SD = 541 s), foraging (mean = 477.7; SD = 183.4) and abnormal behaviour (mean = 458.4; SD = 846.4 s). Further behavioural categories were performed for less than 0.1% of the total observation time (**Figure 1**). Abnormal behaviours were reported in four out of 11 chimpanzees: Tommy was the subject that performed most of these behaviours, spending 9.6% of the total observation time in this activity, followed by Camilla (6.1%), Davidino (2.3%) and Laretta (1.1%).

[Insert Figure 1 here]

Inactivity, activity and not observed

To compare the impact of human exposure on chimpanzees' rearing, we considered hand-reared and mother-reared chimpanzees of the group. In order to investigate differences in activity levels between hand-reared and mother-reared chimpanzees, we compared the duration of being inactive (individual and social resting), active and out-of-sight (not observed). Medians and IQR of inactivity, activity and not observed of hand-reared and mother-reared chimpanzees are reported in **Figure 2**. Mann-Whitney tests revealed no significant differences between hand-reared and mother-reared chimpanzees for inactive behaviour ($U = 238$; $P = 0.936$), active behaviour ($U = 210$; $P = 0.459$) and not observed ($U = 176.5$; $P = 0.126$) (**Figure 2**).

[Insert Figure 2 here]

Individual behaviours

We found no significant differences between hand-reared and mother-reared chimpanzees in individual normal behaviours ($U = 242$, $P = 0.992$) (**Figure 3**). On the other hand, we found a significant difference in abnormal behaviours, that were performed by hand-reared chimpanzees but were absent in mother-reared subjects ($U = 66$, $P < 0.0001$) (**Figure 3**).

[Insert Figure 3 here]

Within individual normal behaviours, we found a significant difference between hand-reared and mother-reared chimpanzees in locomotion that was performed for longer by mother-reared chimpanzees ($U = 138$; $P = 0.015$). On the contrary, self-directed behaviours were performed for significantly longer by hand-reared chimpanzees than mother-reared chimpanzees ($U = 49.5$; $P < 0.0001$) (**Figure 4**). No significant differences were found for other behavioural categories (individual resting: $U = 222$; $P = 0.646$; foraging: $U = 180.5$; $P = 0.153$; individual play: $U = 211$; $P = 0.472$; feeding: $U = 237$; $P = 0.912$; maintenance: $U = 179.5$; $P = 0.144$; visual exploration: $U = 209$; $P = 0.447$) (see **Figure 4** for medians and IQR).

[Insert Figure 4 here]

Social active and passive behaviours

We found a significant difference between hand-reared and mother-reared chimpanzees in overall affiliative behaviours ($U = 172$, $P = 0.103$) whereas we reported no significant differences in overall agonistic behaviours ($U = 201$, $P = 0.342$) (**Figure 3**).

Within social active behaviours (social behaviours performed by the focal subject), we found no significant differences between the two groups considering both affiliative ($U = 172$; $P = 0.103$) and agonistic behaviours ($U = 195$; $P = 0.276$) (**Figure 5**). On the other hand, regarding social passive behaviours (social behaviours received by the focal subject), we found that affiliative behaviours were received for significantly longer by mother-reared chimpanzees than hand-reared chimpanzees ($U = 152.5$; $P = 0.037$) (**Figure 5**). We found no significant differences for agonistic passive behaviours ($U = 217$; $P = 0.562$) and social resting ($U = 192$; $P = 0.246$) (**Figure 5**).

[Insert Figure 5 here]

Discussion & Conclusion

The study chimpanzees performed species-specific individual and social behaviours, while a low degree of abnormal behaviours was also shown by four out of six chimpanzees with atypical early history (Tommy, Camilla, Davidino and Lauretta). Indeed, hand-reared chimpanzees performed significantly more abnormal behaviours than mother-reared subjects, in which these behaviours were absent. Hand-reared chimpanzees, particularly Tommy, were raised primarily under human exposure and had the lowest CHI_i , suggesting that rearing experience can influence the development of the offspring and lead to the display of abnormal behaviours (reviewed by Latham & Mason, 2008). In great apes, hand-rearing has been found to generate undesirable long-lasting effects on behavioural patterns, increasing the performance of stereotypic behaviours even when the animals were then living with peers (Meder, 1989; Marriner & Drickamer, 1994; Nash et al., 1999). However, although we observed apathy and rocking in the study subjects, we did not find any further abnormal behaviour previously described in zoo and laboratory hand-reared chimpanzees. Therefore, although human-mothering might have led to some psychological and behavioural changes in the study hand-reared chimpanzees, its effects seemed to be minimized in the study group.

Within individual behaviours, we also found that hand-reared chimpanzees performed self-directed behaviours for significantly longer than mother-reared subjects. Together with the result on abnormal behaviours, this finding adds to previous studies reporting a long-term increase of stress-related behaviours such as stereotypies and self-directed behaviours in rhesus macaques (*Macaca mulatta*) and chimpanzees with atypical early history and development (Champoux, et al., 1991; Fritz et al., 1992; Spijkerman et al., 1994; Bloomsmith et al., 2002; Latham & Mason, 2008). However, further research should examine a larger sample of chimpanzees with broader rearing histories.

We found that hand-reared and mother-reared chimpanzees show similar behavioural patterns when focusing on overall activity, inactivity and not observed. However, when focusing on different behavioural categories within individual and social behaviours, together with the aforementioned difference in self-directed behaviours, we also found that locomotion was performed significantly more by mother-reared (10% of the total observation time) than hand-reared subjects (7% of the total observation time).

Clearly our data are not comparable with wild conspecifics (see Boesch & Boesch-Achermann, 2000). However, they do represent a similarity to other zoo-housed groups of chimpanzees housed in enclosures with similar locomoting opportunities (Neal Webb et al., 2018). There is some degree of uncertainty around the meaning of increased locomotive behaviour in a zoo setting. Some scholars suggest that it is indicative of positive welfare (Pruetz & McGrew, 2001; Baker et al., 2014) whereas others suggest it to be indicative of tension and anxiety (Baker, 1996; Ross et al., 2010). However, when considering the locomotion data in tandem with more 'typical' stress indicators (*e.g.*, self-directed and abnormal behaviours), it appears that our sample of mother-reared chimpanzees display relatively low levels of stress behaviour (Neal Webb et al., 2018). This implies that the increased locomotion is due to the fact that mother-reared chimpanzees perform more species-typical behaviours than hand-reared chimpanzees, which is indicative of normal behavioural patterns related to a positive welfare status.

In the context of social behaviours, we found that mother-reared chimpanzees performed overall affiliative behaviours for significantly longer than hand-reared chimpanzees. Moreover, mother-reared subjects also received significantly more affiliative behaviours when compared with hand-reared individuals. These findings suggest that chimpanzees with atypical rearing history, experiencing maternal deprivation, might be characterized by poorer social interactions and lack of social competence when compared to mother-reared subjects (*e.g.*, Sanchez, et al., 2001; Ryan, et al., 2002; Kreger et al., 2004; Latham & Mason, 2008; Clay et al., 2015). However, the difference in the time spent performing affiliative behaviours between hand-reared and mother-reared chimpanzees of the current study might be due to the composition of sub-groups within the study colony. Indeed, most of the mother-reared females were related whilst the introduced hand-reared females were unrelated (see Pusey & Schroepfer-Walker, 2013). Additionally, early differences in socialization could have different outcomes for males, such as variations in aggression, competition, and even mating/solicitation behaviours. Thus, the presence of the two males in the hand-reared group might have influenced this result. Further research work is needed to improve our understanding of the actual effect of hand-rearing on

chimpanzee social behaviour by focusing on a larger sample of unrelated male and female animals belonging to different age classes.

Finally, other authors found that housing hand-reared animals in enriched environments and introducing them to conspecifics during the early stages of their development might mitigate the negative effects of maternal deprivation, thus reducing aggression, anti-social behaviours and reproductive incompetence (Hotzel et al., 2004; O'Connell et al., 2005; Tuytens, 2005; Lutz & Novak, 2005); while it is established that adequate enclosure size and positive reinforcement training technique may affect positively the behaviour and welfare of zoo-housed primates (*e.g.*, Spiezio et al. 2015, 2017; Fontani et al. 2014). The study enclosure was large and furnished with climbing structures and vegetation, while the study group was provided with a broad range of environmental enrichments, promoting a wide array of species-specific behaviours in both hand-reared and mother-reared chimpanzees. However, the study sample variance (i.e. including substantial variation in the way the study subjects were treated in early-life) did not enable us to explore whether these social and environmental factors may have contributed to mitigating the effects of maternal deprivation on the behavioural repertoire in the study subjects. Further research work would examine the role played by environmental enrichment when trying to mitigate the negative effects of atypical early-life experiences in zoo-housed chimpanzees.

Our findings suggest that hand-rearing might affect the behaviour of zoo-housed adult chimpanzees. We found significant differences when comparing individual (abnormal and self-directed behaviours, locomotion) and social (affiliative) behaviours of mother-reared and hand-reared female chimpanzees. Therefore, although human intervention may be necessary to ensure the survival of infant chimpanzees in zoos and other captive facilities, minimizing human-animal interactions during their development while providing the opportunity to interact with conspecifics might fill the behavioural gap between human-reared and mother-reared chimpanzees. This approach might promote the performance of species-specific behaviours and adequate intraspecific communication, preventing developmental changes otherwise deriving from the provision of unnatural nursery care.

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Statement of Ethics

The study was carried out through the behavioural observation of the chimpanzee group, using non-invasive techniques. The study procedure was in accordance with the EU Directive 2010/63/EU and the Italian legislative decree 26/2014 for Animal Research. No special permission to use animals in the current ethological non-invasive study is required, as zoological gardens in Italy are expected to carry out behavioural observations of the individuals in their care, in order to guarantee the animal welfare (D. Lgs.73/2005).

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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The authors have not received any funding relevant to this study.

Author Contributions

Caterina Spiezio designed the study and carried out the statistical analyses. Stefano Vaglio contributed to the interpretation of the results and co-wrote the paper. Camille Vandelle conducted the data collection. Camillo Sandri assisted with the development of the ideas and the interpretation of the results. Barbara Regaiolli contributed to the statistical analyses, assisted with the interpretation of the results and co-wrote the paper.

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Figure Legends

Figure 1: Normal and abnormal behaviours performed by the study chimpanzees. Mean time spent by the entire group of chimpanzees (both HR and MR individuals) performing different behaviours described in **Table 2**.

Figure 2: Duration of inactivity, activity and not observed in HR and MR chimpanzees.

The horizontal lines within the box indicate the medians, boundaries of the box indicate the first and third quartile. The x inside the box indicates the mean. The whiskers extend up from the top of the box (upper quartile) to the largest data element that is less than or equal to 1.5 times the interquartile range (IQR) and down from the bottom of the box (lower quartile) to the smallest data element that falls within a distance of 1.5 times the IQR. Values outside this range are considered outliers and are drawn as points.

Figure 3: Duration of individual behaviors (normal and abnormal) and social behaviours (affiliative and agonistic) in HR and MR chimpanzees. The horizontal lines within the box indicate the medians, boundaries of the box indicate the first and third quartile. The x inside the box indicates the mean. The whiskers extend up from the top of the box (upper quartile) to the largest data element that is less than or equal to 1.5 times the interquartile range (IQR) and down from the bottom of the box (lower quartile) to the smallest data element that falls within a distance of 1.5 times the IQR. Values outside this range are considered outliers and are drawn as points. * $P < 0.05$; *** $P < 0.0001$.

Figure 4: Duration of different individual behaviours in HR and MR chimpanzees

(Ind.Rest = individual resting; Ind.Play = individual play; Locom = locomotion; Mainten. = maintenance; Vis-Expl. = visual exploration; Self = self-directed behaviours). The horizontal lines within the box indicate the medians, boundaries of the box indicate the first and third quartile. The x inside the box indicates the mean. The whiskers extend up from the top of the box (upper quartile) to the largest data element that is less than or equal to 1.5 times the interquartile range (IQR) and down from the bottom of the box (lower quartile) to the smallest data element that falls within a distance of 1.5 times the IQR. Values outside this range are considered outliers and are drawn as points. * $P < 0.05$; *** $P < 0.0001$.

Figure 5: Duration of different social active and passive behaviours in HR and MR chimpanzees.

The horizontal lines within the box indicate the medians, boundaries of the box indicate the first and third quartile. The x inside the box indicates the mean. The whiskers extend up from the top of the box (upper quartile) to the largest data element that is less than or equal to 1.5 times the interquartile range (IQR) and down from the bottom of the box (lower quartile) to the smallest data element that falls within a distance of 1.5 times the IQR. Values outside this range are considered outliers and are drawn as points. * $P < 0.05$; *** $P < 0.0001$.