EARLY LIFE EXPERIENCES: ACTIVITY LEVELS AND ABNORMAL BEHAVIOURS IN RESOCIALISED CHIMPANZEES

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Abstract

*Chimpanzees (*Pan troglodytes*) that are kept in captivity come from a wide variety of backgrounds, and a proportion of them have been subjected to maternal separation and social deprivation during development. The long-term effects of such practices have received little investigation. This study investigates whether the removal of infants from their mothers and/or other chimpanzees affects their activity levels and abnormal behaviours later in life. A total of 69 resocialised chimpanzees were studied at six zoos in the United Kingdom. Chimpanzees were categorised into one of three rearing conditions: reared by their mother in a group of conspecifics (MGR); reared with other conspecifics but separated from their mothers (RO); and reared apart from their mother or other conspecifics for a period of time during infancy (RA). Results indicate that 'socially deprived' individuals show reduced levels of normal activity, elevated levels of abnormal behaviours and a wider repertoire of abnormal behaviours. These differences were more pronounced in younger individuals, with adults from the three different rearing conditions performing abnormal behaviour patterns at comparable levels. It is concluded that human-rearing, either alone or with conspecifics, influences behaviour through suppression of normal activity levels as a result of separation and elevation of levels of abnormal behaviours as a mechanism for coping with maternal loss and restricted rearing. However, these effects are not irreversible and recovery of 'normal' behaviours may occur with access to an enriched social environment.*

Keywords: *abnormal behaviours, activity, animal welfare, chimpanzees, early experience*

Introduction

Over the years, humans have used chimpanzees in numerous ways — as pets, photographers' aids, performers, zoo exhibits and research subjects in laboratory studies. For several of these applications, infants are used exclusively, being obtained through captive breeding or capture from wild groups (which is now illegal). Initially, infants are manageable and appealing, but with maturity they become too big and strong to be handled. This leads to the problem of housing maternally deprived chimpanzees for the rest of their lives, which may be up to 50 years. Today there are many chimpanzees in captivity which, although now resocialised, were removed from their mothers as infants for human use. These individuals have been subjected to varying degrees of social deprivation, but all have lost opportunities to learn and experience relationships with their mother and with other group members at a crucial stage of their development.

In the 1950s and 1960s, many studies investigated the effects of social deprivation on the behaviour of laboratory primates (Harlow 1959; Harlow & Harlow 1962a,b; Davenport & Menzel 1963; Mason 1965; Sackett 1967; Berkson 1968). Maternal deprivation was a topic of much research, as psychologists, psychiatrists and psychoanalysts were interested in the disruption of the mother–infant bond in human infants and the influence that this had on later behaviour and personality (Harlow 1959; Harlow & Harlow 1962a,b; Chamove *et al* 1972). Because of the moral restrictions of carrying out deprivation studies on humans, primate studies were performed to investigate the factors that influence the development of attachments (Harlow & Harlow 1962b), and chimpanzees were used as subjects in a number of studies.

As in other primate species, maternal separation in chimpanzees results in the development of abnormal behaviours (Harlow & Harlow 1962b; Davenport & Menzel 1963; Mason 1965; Berkson 1968; Dienske & Griffin 1978; Chamove *et al* 1984). Stereotypies in isolation-reared chimpanzees are common and take the form of rocking or swaying, repetitive movements of individual body parts (eg head banging) and 'posturing', such as holding a hand in front of the eyes (Davenport & Menzel 1963). Davenport *et al* (1966) found that chimpanzees reared from birth in social isolation develop at least one stereotyped behaviour and may go on to develop as many as eight different stereotypies. Walsh *et al* (1982) described the abnormal behaviour of restricted-reared chimpanzees as idiosyncratic, with individuals developing their own "expression of psychological disturbance" (Walsh *et al* 1982, p 318). Nursery-reared infants have been shown to develop abnormal behaviours, but to a lesser extent than isolation-reared infants. They show the redirected clasping (self- or peer-), self-sucking (digits) and repetitive body movements described in other primate species (Dienske & Griffin 1978). However, digit sucking was only observed in nursery-reared infants who had spent less than a month with their mother after birth.

In Spijkerman *et al*'s (1994) study on body rocking in chimpanzees aged 0–10 years, mother- and group-reared chimpanzees were never observed to rock. However, most (33 out of 36) developed rocking if separated from their mother shortly after birth and raised in an incubator. If separated from their mother later in life (after three months of age), rocking was more likely to develop in infants placed in a peer group without a familiar peer or 'friend'. A lack of availability of body contact from a 'friend' was identified as being the causal factor. Rocking was also found to develop as soon as it was physically possible (at around 90 days of age). In addition, it was found that 'rockers' coped better with stress, by maintaining less body contact with a conspecific and playing more than 'non-rockers'. Qualitative observations by Fritz noted that chimpanzees which rock never become dominant animals or predictable breeders. In addition, rocking inhibits exploratory behaviour in infant and juvenile chimpanzees (Fritz & Fritz 1985). The information on rocking in chimpanzees supports that documented for humans. In humans, stereotypic rocking is well-documented in individuals with mental retardation, pervasive developmental disorders such as autism, and severe sensory deprivation such as blindness and deafness (cf DSM-IV 1995; Prior & Ozonoff 1998). In addition, it is seen in individuals in institutional environments in which the individual receives insufficient stimulation (cf DSM-IV 1995) and in children under stress (such as from exam pressure; Connor 2001). For both chimpanzees and humans, rocking appears to be a coping mechanism which acts to balance out levels of stimulation to levels that allow the individual to deal with both under- and over-stimulation.

There are some indications that chimpanzees are able to show a higher degree of recovery from separation than some primate species, such as the rhesus macaque (*Macaca mulatta*). For example, thumb sucking is less common and not as persistent in chimpanzees as it is in

rhesus macaques (Mason *et al* 1968). Davenport *et al* (1966) found that chimpanzee infants tolerated six months of social and sensory isolation and showed no stereotypies. However, these infants had been mother-reared for the first year of life and had subsequently been housed with peers before the commencement of isolation at 18 months of age. In addition, in contrast to studies of monkeys and other animals, repetitive locomotor stereotypies have not been observed in chimpanzees, regardless of the conditions in which they were reared (Spijkerman *et al* 1994). Spijkerman *et al* (1995) found that in peer-reared infants the performance of rocking did not influence the amount of social play performed, with no observed difference in amounts of social play between rockers and non-rockers.

Other studies have shown that apes' responses to maternal separation may be more similar to those observed in human infants than monkeys' responses. In Codner and Nadler's (1984) study on the process of separation and reunion in three species of great ape, they distinguished phases of 'protest' and 'despair' as seen in monkey studies, but they also identified a brief period of detachment on reunion that can be seen in human infants (cf Bowlby 1973). In addition, they found that the initial agitation phase at the time of maternal separation was longer than that seen in monkeys. Bard and Nadler (1983) also reported that the 'protest' phase was more like that seen in children than that observed in monkey studies.

Problems with interpreting traditional deprivation studies arise from two substantial differences between mother- and human-rearing. Under deprivation conditions, not only is the social environment deprived but the physical environment is often impoverished. In many of the original experiments, isolation-reared infants were housed in bare empty cages, with some studies using housing with a high degree of sensory deprivation (cf Harlow & Harlow 1962a,b; Davenport & Menzel 1963; Davenport *et al* 1966; McKinney *et al* 1971; Chamove *et al* 1973). In some cases, the control groups were not housed in such extreme poverty. This makes distinguishing between the effects of social deprivation and the influence of environmental conditions difficult. Secondly, decreases in activity levels and other behavioural changes during separation, obtained in earlier studies, could be due to a decrease in available space in isolation housing (cf Bard & Nadler 1983; Snyder *et al* 1984). Environmental conditions have been documented as influencing the behaviour of chimpanzees (Maple & Stine 1982; Traylor-Holzer & Fritz 1985; Brent *et al* 1991; Matevia *et al* 1991).

Many of the previous deprivation studies involved extreme sensory and environmental deprivation, investigated short-term effects only, or were concerned only with behaviours that affect captive breeding, such as aggression and reproduction (Harlow & Harlow 1962a,b; Davenport & Menzel 1963; Davenport *et al* 1966; McKinney *et al* 1971; Chamove *et al* 1973). This study compares the behaviour of socially deprived chimpanzees with counterparts that had been reared in a 'naturalistic' setting with their mother and other group members. Although the deprived individuals were resocialised in enriched environments, the long-term effects of their background on their behaviour are not fully understood. The present study addresses the question of whether the behavioural differences between socially deprived and mother-reared individuals remain when deprived chimpanzees are resocialised in suitable physical and social environments. Many zoos today, and all of those which took part in this study, are constantly striving to improve the life of captive chimpanzees in their care and are concerned that individuals with an abused background have more specific needs. All zoos involved in this study have never, or not for many years, practised maternal separation of infants unless no other options were available to them. In addition, one zoo — Monkey World — actively and successfully specialises in rescuing and resocialising chimpanzees from inappropriate backgrounds.

Methods

Subjects

Sixty-nine chimpanzees (23 male, 26 female) from six different UK zoos (Belfast Zoo, Chester Zoo, Edinburgh Zoo, Monkey World [MW], Penscynor Wildlife Park and Whipsnade Wild Animal Park) were studied between March 1994 and April 1998. Twenty-eight of the chimpanzees had been reared by their mother in a social group (mother- and group-reared, MGR); 12 had been separated from their mother as dependent infants and human-reared with other conspecifics (reared with other conspecifics, RO); and 29 had been subjected to a period of time separated from their mother and other chimpanzees whilst dependent infants (reared apart, RA). Because of the limited knowledge about most rescued chimpanzees, details of how long RA chimpanzees had been subjected to social separation were unobtainable. The age range of the subjects was 2–50 years, and individuals were assigned to one of three age categories adapted from Fritz and Howell's (1993) classification of captive chimpanzees (see Table 1). All groups were housed in large indoor and outdoor enclosures, although there was a large range of sizes (see Table 2 for area available per individual). Zoos were chosen for their similarity in management styles in order to reduce confounding variables. However, the management of the groups did vary to some extent with location. For example, some groups were shut into their indoor enclosure at night whereas others had 24 h access to all areas. However, none of the groups were split into subgroups throughout the course of the study, a process which is thought to cause management problems (Catlow *et al* 1998). The environmental properties of each location are given in Table 2.

Table 1   **Age categories used in this study.**

Age category	Age range (years)	Description
1 (n = 22)	2–7	Infants and juveniles
2 (n = 19)	8–15	Adolescents and young adults
3 (n = 28)	16+	Prime, mature and old adults

Table 2   **Social and physical environmental variables.**

	Chester	MW	Belfast	Edinburgh	Whipsnade	Penscynor
No. animals studied	22	15	10	10	7	5
Group size	25	15	13	12	9	5
No. age 1	10 (40%)	8 (53%)	7 (54%)	4 (33%)	3 (33%)	0
No. age 2	2 (8%)	5 (33%)	3 (23%)	1 (8%)	3 (33%)	5 (100%)
No. age 3	13 (52%)	2 (13%)	3 (23%)	7 (54%)	3 (33%)	0
No. MGR	14 (56%)	0	11 (85%)	7 (58%)	6 (66%)	0
No. RO	7 (28%)	0	0	2 (17%)	0	2 (40%)
No. RA	4 (16%)	15 (100%)	2 (15%)	3 (25%)	2 (22%)	3 (82%)
No. males	5 (20%)	4 (27%)	4 (31%)	7 (58%)	6 (67%)	2 (40%)
No. females	20 (80%)	11 (73%)	9 (69%)	5 (42%)	3 (33%)	3 (60%)
Stability (years)*	4	<1	11	5	16	4
Area (m^2 per animal)	103.9	434.9	243.1	109.6	277.3	72.8
No. feeds per day	3	2	3	5+	3	1

*Stability = number of years since last introduction or removal of an individual from the group by means other than birth or death.

Behavioural observations

Continuous recordings from 15 min sample periods were made on focal individuals. Sample allocation was achieved using a repeated Latin Square design to ensure that all time periods throughout the study sessions (1000h–1600h) were equally sampled. Recordings were not

made outside this time period as most zoos carried out management practices (eg cleaning and moving groups), which influenced behaviour patterns and social dynamics, outside peak visitor periods. A total of 3 h observation was obtained for each focal animal. Three behavioural categories were recorded: normal activity, inactivity, and abnormal behaviour. Normal activity was defined as all behaviours except when the chimpanzee was stationary, lying down or performing abnormal behaviours. Normal activity therefore included all social and solitary behaviours that involved the individual actively performing an action, including all agonistic and grooming behaviours (these had previously been assessed to be at normal non-pathological levels; Martin 2000). Inactivity was defined as all stationary and resting/sleeping behaviours. Abnormal behaviour was classified into one of seven types (adapted from Walsh *et al* 1982):

1. *Eat non-edible*: consume any object which was not a food item
2. *Faecal manipulation*: any manipulation of faeces, such as smearing or ingestion
3. *Masturbate*: manual stimulation of genitals
4. *Rock*: any stereotypic rocking movements
5. *Self-injure*: inflict injury or potential injury on own body
6. *Self-suck*: suck part of own body
7. *Spit*: spit on a surface (eg window), and may be accompanied by smearing or licking.

These categories included behaviours that are rarely observed in wild chimpanzees (eg masturbation; Goodall 1986) and were therefore considered to be abnormal in the sense that they could be attributed to some influence of the captive environment.

For each individual, mean values for total frequency and total time of normal activity, inactivity and abnormal behaviour were obtained for the twelve 15 min samples, along with the total frequency of each class of abnormal behaviour. Therefore all data obtained were for a total of 3 h of observation.

Statistical analysis

Non-parametric techniques were used because the assumptions for parametric testing were not met. The data did not display normality and homogeneity of variance, and were skewed with unequal sizes of cells. For comparisons between two independent groups, the Mann-Whitney U test for independent samples was used, and for comparisons between three or more groups, Kruskal-Wallis one-way analysis of variance was used. In all cases, the appropriate multiple comparisons (as described by Siegel & Castellan 1988) were used to identify differences between treatments when the Kruskal-Wallis test result was found to be significant. Spearman's rank order correlation coefficient was used to test for relationships between two variables. Two-tailed tests were used, and differences where $P < 0.05$ were considered statistically significant.

Results

Levels of normal activity

Chimpanzees who were mother-raised (MGR) (median = 506.30 s [interquartile range = 174.67], n = 28) spent longer, in total, in normal activity than animals in either of the other two rearing conditions (reared with other conspecifics [RO]: median = 363.85 s [range = 204.11], n = 12; reared apart [RA]: median = 352.47 s [range = 181.18], n = 29; Kruskal-Wallis: Chi^2 = 11.96, $P = 0.003$). Four individuals spent very little time active and had average total times for normal activity of less than 200 s per 900 s (15 min) sample. All had suffered some degree of deprivation during childhood. Of these four, both Tom (Edinburgh Zoo) and Fergus (Penscynor Wildlife Park) were RO males, aged 19 and 12

years respectively, and had normal activity total times of 198 s and 162 s respectively. Lola (seven-year-old RA female at Monkey World) spent, on average, a comparatively low total time active (191 s), but Suzi (14-year-old RA female at Penscynor Wildlife Park) had extremely low levels, spending on average a total of 80 s active per sample. RA infants were more frequently active (median = 15.96 s [range = 3.44], n = 8), but spent less time in normal activity (median = 465.42 s [range = 67.02]) than MGR peers (frequency: median = 11 [range = 2.33], n = 14; Kruskal-Wallis: $Chi^2 = 3.92$, $P = 0.048$; total time: median = 575.9 s [range = 100.26], n = 14, Kruskal-Wallis: $Chi^2 = 7.45$, $P = 0.006$). MGR adolescents and young adults (median = 429.67 s [range = 61.37], n = 9) showed a trend towards longer total times spent active than their deprived-rearing peers (RO: median = 218.67 s, n = 2; RA: median = 310.89 s [range = 39.41], n = 8; Kruskal-Wallis: $Chi^2 = 6.71$, $P = 0.035$). However, prime, mature and old adults did not differ across rearing conditions for any of the measures of normal activity. In this age group, the level of normal activity did not differ between rearing conditions.

The location of individuals also had a significant effect on the frequency and total time of normal activity (Table 3). However, all of the differences between the different zoo groups could be attributed to differences in age composition within these groups, and no differences between zoos were found when each age class was compared individually (Figure 1).

Table 3   **Frequency and total time of normal activity for zoo.**

Zoo	Median frequency (interquartile range)	Median total time (interquartile range)
Chester (n = 22)	8.38 (6.08)[a,b]	468.60 (176.52)[a]
Monkey World (n = 15)	11.67 (7.33)[a]	352.47 (159.67)[a,b]
Belfast (n = 10)	8.71 (1.19)[a,b]	462.92 (175.44)[a,b]
Edinburgh (n = 10)	6.92 (5.27)[a,b]	416.83 (150.86)[a]
Whipsnade (n = 7)	6.83 (2.50)[b]	524.42 (233.33)[a]
Penscynor (n = 5)	7.58 (4.04)[a,b]	261.33 (164.25)[b]
Significance	$Chi^2 = 13.25$ (Kruskal-Wallis), $P = 0.021$	$Chi^2 = 14.91$ (Kruskal-Wallis), $P = 0.011$

Median values with different superscripts are significantly different ($P < 0.05$), ie median frequency: Monkey World > Whipsnade; median total time: Chester, Edinburgh and Whipsnade > Penscynor.

Levels of abnormal behaviour

The number of chimpanzees showing abnormal behaviours was found to vary between rearing conditions ($Chi^2 = 12.90$, $df = 6$, $P = 0.045$), with RA individuals being more likely to perform abnormal behaviours frequently and MGR individuals being more likely never to perform abnormal behaviours (Table 4). Almost two thirds of all RA group members showed abnormal behaviours once or more; on the other hand, for the other two rearing groups, around one third of individuals showed abnormal behaviours once or more (Table 4). Nearly one fifth of the RA chimpanzees showed abnormal behaviours 10 times or more in the total recording period (3 h) whereas only one RO individual, Wilson, a 26-year-old male at Chester Zoo, showed abnormal behaviours at this frequency.

Rearing condition had a significant effect on the levels of abnormal behaviour observed. Although no one condition was found to be statistically different from the others (using the multiple comparison method), Table 5 shows that RA chimpanzees had a tendency for higher levels of abnormal behaviour than MGR chimpanzees. Four individuals had exceptionally high levels of abnormal behaviour, spending on average over 50 s (5.6%) in some form of abnormal behaviour per 900 s sample. Three were RA females: Lola, a seven-year-old at Monkey World, spent on average 76 s performing abnormal behaviours; Neusi, a 13-year-old at Penscynor Wildlife Park, spent 77 s; and Athena, a three-year-old at Monkey World,
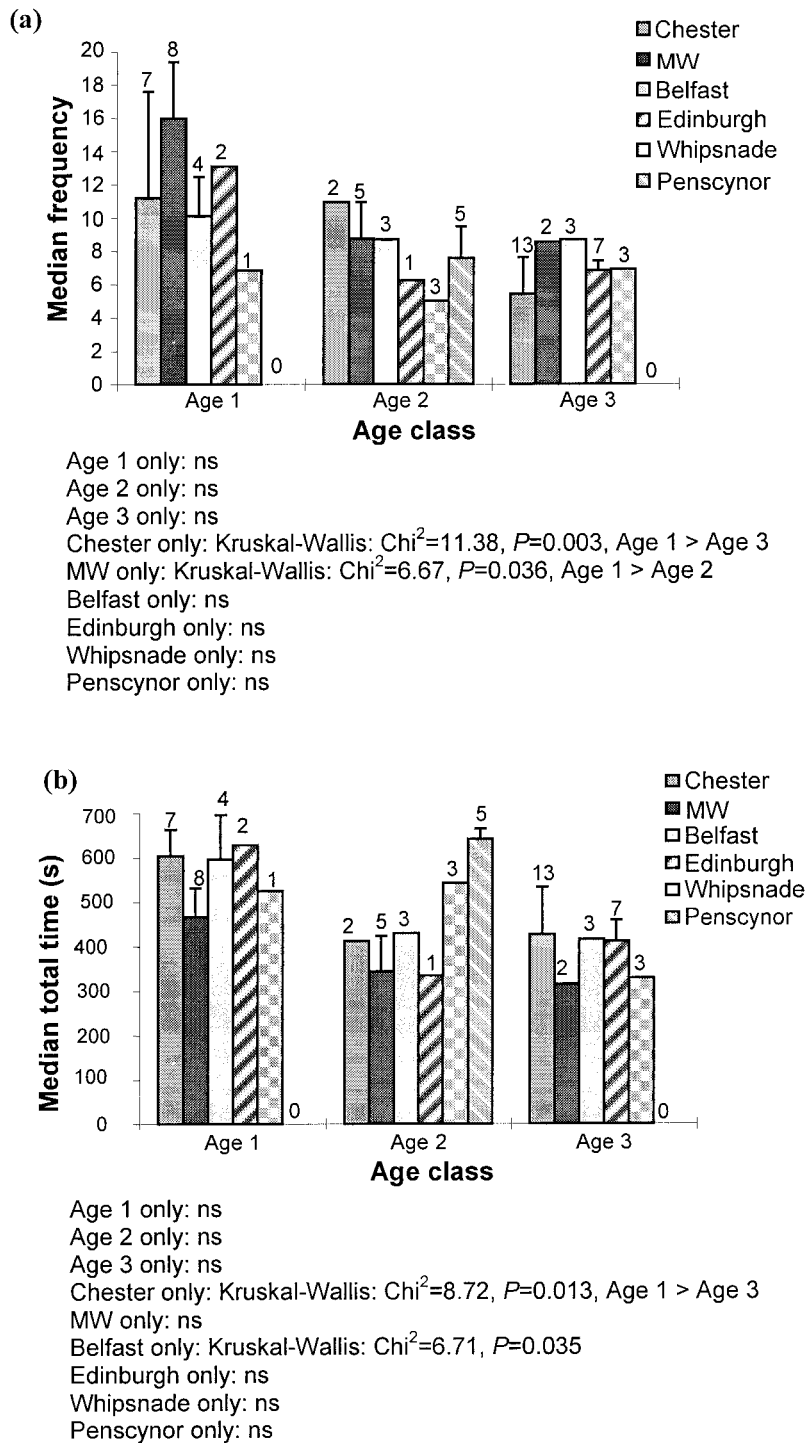
(a)

Age 1 only: ns
Age 2 only: ns
Age 3 only: ns
Chester only: Kruskal-Wallis: Chi^2=11.38, P=0.003, Age 1 > Age 3
MW only: Kruskal-Wallis: Chi^2=6.67, P=0.036, Age 1 > Age 2
Belfast only: ns
Edinburgh only: ns
Whipsnade only: ns
Penscynor only: ns

(b)

Age 1 only: ns
Age 2 only: ns
Age 3 only: ns
Chester only: Kruskal-Wallis: Chi^2=8.72, P=0.013, Age 1 > Age 3
MW only: ns
Belfast only: Kruskal-Wallis: Chi^2=6.71, P=0.035
Edinburgh only: ns
Whipsnade only: ns
Penscynor only: ns

Figure 1   **The effects of zoo and age class on normal activity.**

spent 92 s. Wilson, a 26-year-old RO male at Chester Zoo, showed the highest level of abnormal behaviour, spending on average 106 s per sample. Both Neusi and Wilson also showed high frequencies of abnormal behaviours, being the only two individuals with average rates higher than 2 per sample (6.3 and 2.4, respectively).

Table 4 Percentage (and number) of individuals in each rearing condition observed performing abnormal behaviours.

	MGR (n = 28)	RO (n = 12)	RA (n = 29)
Never	61% (17)	75% (9)	38% (11)
1–4 times	36% (10)	17% (2)	28% (8)
5–9 times	3% (1)	0	17% (5)
≥10 times	0	8% (1)	17% (5)

**Table 5** Frequency and total time of abnormal behaviour for rearing condition.

Rearing	Median frequency (interquartile range)	Median total time (interquartile range)
MGR (n = 28)	0 (0.08)	0 (1.90)
RO (n = 12)	0 (0.13)	0 (2.00)
RA (n = 29)	0.08 (0.54)	12.25 (37.17)
Significance	$Chi^2 = 7.44$ (Kruskal-Wallis), $P = 0.024$	$Chi^2 = 6.26$ (Kruskal-Wallis), $P = 0.044$

When rearing and age were compared together, infant and juvenile animals were found to be the most affected by their background, with animals in this age class (Age 1) only showing a significant increase in levels of abnormal behaviours as deprivation increased (Figure 2). It was thought that a zoo effect could have been responsible for these differences, as the zoos were not equally represented across rearing conditions. However, Figure 2 shows a large amount of variation for RA infants and juveniles. All of these chimpanzees were housed at Monkey World. For the MGR individuals, however, there was very little spread or variability, even though they were represented at four different locations (Belfast, Chester and Edinburgh Zoos, and Whipsnade Wild Animal Park).

Levels of abnormal behaviours varied with location, with chimpanzees at Penscynor Wildlife Park and Monkey World showing higher levels than those at the other zoos, particularly Chester and Edinburgh Zoos (Table 6). This would be expected if rearing condition had an effect, as all of the Penscynor and Monkey World chimpanzees were from deprived backgrounds. In an attempt to identify confounding variables, abnormal behaviour measures for each zoo group were correlated with each of the different environmental features described in Table 2. There were very few significant correlations. However, both frequency and total time of abnormal behaviours were found to correlate negatively with the number of feeds received per day ($r_s = -0.826$, n = 6, $P = 0.043$) and with the percentage of MGR individuals ($r_s = -0.823$, n = 6, $P = 0.044$), and positively with the percentage of RA individuals ($r_s = 0.845$, n = 6, $P = 0.034$). Stability and area available per individual were not related to levels of abnormal behaviours.

Types of abnormal behaviour

If MGR individuals showed any abnormal behaviours, then they were only ever seen performing one type of abnormal behaviour (Table 7). For RA chimpanzees, however, over 40% of individuals performed two or more different abnormal behaviours. This suggests that with increased deprivation, a greater variety of abnormal behaviours are seen in the individual's repertoire. More variety in abnormal behaviours was seen for the group as a

(a)
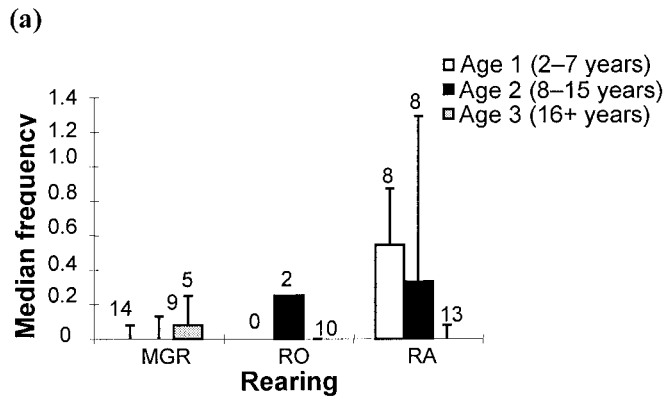
Age 1 only: Kruskal-Wallis: Chi^2=4.94, P=0.026
Age 2 only: Kruskal-Wallis: Chi^2=6.06, P=0.048
Age 3 only: ns
MGR only: ns
RO only: ns
RA only: ns

(b)
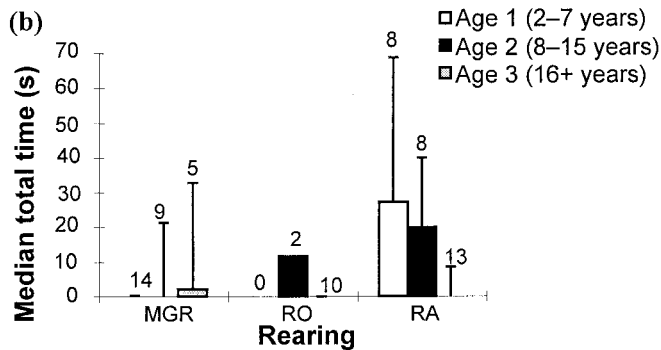
Age 1 only: Kruskal-Wallis: Chi^2=4.93, P=0.026, RA>MGR
Age 2 only: ns
Age 3 only: ns
MGR only: ns
RO only: ns
RA only: ns

Figure 2   The effects of rearing condition and age class on abnormal behaviour.

whole for RA chimpanzees (Table 8a). The location of the group had little effect on variation with the exception of Monkey World, which showed many more abnormal behaviours than any other group (Table 8b). This was probably because the individuals came from a much wider range of backgrounds (eg laboratories, circuses and Spanish beaches) and had the largest number of RA individuals.

Table 6   Frequency and total time of abnormal behaviour for zoo.

Zoo	Median frequency (interquartile range)	Median total time (interquartile range)
Chester (n = 22)	0 (0.08)[a,c]	0 (3.31)[a,b]
MW (n = 15)	0.33 (0.75)[a,b]	14.58 (41.21)[a]
Belfast (n = 10)	0 (0.08)[a,b,c,d]	0 (0.46)[a,b]
Edinburgh (n = 10)	0 (0.02)[c]	0 (0.52)[b]
Whipsnade (n = 7)	0 (0.58)[a,b,c,d]	0 (38.08)[a,b]
Penscynor (n = 5)	0.33 (3.17)[b,d]	20.50 (38.17)[a]
Significance	Chi^2 = 20.63 (Kruskal-Wallis), $P = 0.001$	Chi^2 = 17.52 (Kruskal-Wallis), $P = 0.004$

Mean values with different superscripts are significantly different ($P < 0.05$), ie median frequency: Monkey World > Edinburgh, Penscynor > Chester and Edinburgh; median total time: Monkey World and Penscynor > Edinburgh.

Table 7   Percentage (and number) of different types of abnormal behaviours performed by individuals in each rearing condition.

	MGR (n = 28)	RO (n = 12)	RA (n = 29)
One	39% (11)	17% (2)	21% (6)
Two	0	8% (1)	31% (9)
Three	0	0	10% (3)

The results presented in Table 8a suggest that RA chimpanzees showed higher frequencies of faecal manipulation compared to other rearing conditions, although this behaviour was common over all rearing conditions. Both RA and RO chimpanzees showed high frequencies of rocking, which was not seen at all in MGR individuals. However, this high rate of rocking was caused by two high scores: Wilson, a RO male at Chester Zoo, was seen to rock 29 times over the 3 h of observation; and Neusi, a RA female at Penscynor Wildlife Park, rocked 75 times. This pushed up the rate of rocking for these categories. Apart from rocking and faecal manipulation, all other abnormal behaviours were performed at low rates. Faecal manipulation was the most common, or the second most common (with rocking being the first) for all rearing conditions and was also seen at all zoos (Table 8b). Twenty-six out of the 69 chimpanzees observed were recorded to perform faecal manipulation once or more (only nine showed rocking behaviours). This suggests that the zoo environment could be a contributory factor to the occurrence of this abnormal behaviour, because it is rarely performed in the wild.

Discussion

Levels of activity appeared to be higher in MGR chimpanzees than in either RO or RA chimpanzees. Rearing condition had the greatest effect on infants and juveniles, with prime, mature and old adults showing little difference in normal activity levels between rearing conditions. RA infants showed a greater frequency of normal activity than their MGR peers. They also showed lower normal activity total times. The high frequency of activity in RA youngsters is probably related to the high levels of play consistently observed in young chimpanzees both in captivity (Spijkerman et al 1995; Martin 2000) and in the wild (Goodall 1986). Although in an earlier study (Martin 2000) no difference was found in levels of play between non-deprived and deprived infants, other active behaviours may have been suppressed. Therefore, high activity frequencies for RA youngsters may relate to normal play levels but the lower total time spent active reflects suppressed general activity. From these

Table 8   Mean frequency per group member of types of abnormal behaviours.

(a) Rearing condition

Type of abnormal behaviour	MGR (n = 28)	RO (n = 12)	RA (n = 29)
Eat non-edible	0.64	0	0.31
Faecal manipulation	0.57	0.41	1.79
Masturbate	0.14	0	0.38
Rock	0	2.5	3.41
Self-injure	0.04	0	0.03
Self-suck	0	0	0.17
Spit	0	0	0.21

(b) Zoo

Type of abnormal behaviour	Chester (n = 22)	Monkey World (n = 15)	Belfast (n = 10)	Edinburgh (n = 10)	Whipsnade (n = 7)	Penscynor (n = 5)
Eat non-edible	0.14	0.60	0	0	0	0
Faecal manipulation	0.32	2.67	0.50	0.40	1.14	2.2
Masturbate	0	0	0	0.40	1.57	0
Rock	1.32	0.60	0	0	0	0
Self-injure	0	0.07	0.10	0	0	0
Self-suck	0	0.20	0	0	0	0.40
Spit	0	0.40	0	0	0	0

results, it can be seen that frequency and duration of behaviour are not equivalent measures of activity. The absence of RO infants and juveniles within this study meant that the effect of severity of deprivation could not be assessed. This lack of available subjects was most likely to be a result of changes in management practices in recent years, with zoos no longer housing infant chimpanzees in nursery groups. However, similar results have been found for juvenile chimpanzees, with those reared in peer groups having lower levels of activity than those reared in a large social group (Bloomsmith *et al* 1991, cited in Spijkerman *et al* 1997).

The longer total times seen in normal activity for MGR infants compared to RA infants might suggest that the earlier trauma of separation from the mother is still affecting their behaviour. The total time spent active by adolescents was related to their background, with RO and RA individuals having shorter normal activity times than their MGR peers. However, this effect was not as strong as it had been for the infants and juveniles. In addition, the lack of difference in normal activity times between adults suggests that as age increases, normal activity levels are restored to those of 'normal' chimpanzees. This could be a result of an enriched environment and/or the presence of non-deprived 'therapist' chimpanzees. Prime mature and old adults, in general, showed no effects of deprivation in their levels of normal activity, suggesting that recovery can occur.

Why do deprived individuals demonstrate reduced activity levels? It is likely that some form of depression or emotional apathy results from maternal separation and restricted rearing. The occurrence of depression in orphaned chimpanzees is well documented (van Lawick-Goodall 1968; Goodall 1983, 1986, 1989; Hiraiwa-Hasegawa & Hasegawa 1988) and can result in illness and death. Wild orphans that survive show a slow recovery from this depression. In this study, recovery of normal activity levels appeared to occur with increased age and, therefore, increased time in an enriched, social environment. Learned helplessness (Seligman 1975), or the perception of uncontrollable stress, has been found to produce cognitive deficits, emotional changes and a reluctance to initiate action, and is related to depression in humans (Mook 1987). In prisoners of war, whose environmental conditions may not be very far removed from those experienced by primates separated from their

mothers and/or peers, withdrawal and apathy have been documented (Strassman *et al* 1956). In humans, prolonged stress with which the individual is unable to cope results in apathy and may progress to depression, especially if the individual learns that their responses to the stressor are useless in controlling it; however, as in chimpanzees, there seem to be individual differences in human responses to stress (Atkinson *et al* 1996).

A limited effect of zoo location was found on normal activity levels, with any differences being attributable to differences in composition of age groups. This suggests that although each zoo's management of their group varied, no one location had elevated or depressed activity levels induced by physical environmental factors. Therefore, an enriched, social environment can be achieved in a variety of ways. However, other studies have reported changes in activity levels related to changes in the physical environment (Nieuwenhuijsen & de Waal 1982; Brent *et al* 1991) and in management techniques (Paquette & Prescott 1988; Bloomsmith & Lambeth 1995).

Deprivation during upbringing was shown to be related to the levels of abnormal behaviours, with individuals who had suffered a period of total separation (RA) showing the highest levels. This supports results (Davenport *et al* 1966; Dienske & Griffin 1978; Fritz *et al* 1992b; Marriner & Drickamer 1994) demonstrating that socially deprived individuals show higher levels of abnormal behaviours. These results also suggest that even when in a socially and physically enriched environment, abnormal behaviours remain and are resistant to change. For example, Wilson at Chester Zoo still rocked after spending 14 years in a large social group. Rocking in resocialised chimpanzees has been observed by other authors (Fritz 1989); however, it does not prevent the occurrence of normal behaviours (Fritz *et al* 1992b).

As with normal activity levels, recovery to levels of abnormal behaviour comparable with 'normal' captive chimpanzees seemed to have occurred in many older individuals. Reduction in abnormal behaviours has been documented in socially deprived chimpanzees that have been rehoused in social groups or in enriched environments (Wilson & Elicker 1976; Pfeiffer & Koebner 1978; Clarke *et al* 1982; Hannah & McGrew 1991; Agoramoorthy & Hsu 1999) or that have been subjected to resocialisation procedures (Fritz & Fritz 1979).

Not only did rearing condition affect the levels of abnormal behaviours, but a deprived upbringing increased the likelihood of showing any abnormal behaviours and increased the range of different abnormal behaviours. As in other studies on abnormal behaviour in chimpanzees (Spijkerman *et al* 1994), and unlike monkey studies (cf Berkson 1968), no repetitive locomotor stereotypies were observed. Rocking behaviours were more common in deprived (RO and RA) individuals, and self-sucking and spitting were only seen in RA individuals. Spitting and licking saliva off walls has been observed in laboratory-housed chimpanzees, which performed this repetitive act for 5–10 min at a time (Kollar *et al* 1968). Fritz *et al* (1992b) found that hand-reared chimpanzees were more likely to rock (40% of individuals) than individuals who had been mother-reared for at least 12 months (16.5% of individuals). Spijkerman *et al* (1994) investigated rocking behaviour in 90 chimpanzees under the age of 10 years. Mother- and zoo-reared youngsters were never seen to rock. For separated youngsters, they found a large amount of individual variation. Animals over the age of two years that did rock spent around 3–4% of time rocking, with levels of rocking remaining consistent for individuals. As pointed out by Spijkerman *et al* (1994), once rocking becomes habitual it is seen even in the absence of stress and frustration, with levels doubling at times of stress.

The MGR prime, mature and old adult group appeared to display higher levels of abnormal behaviours (Figure 2) and a higher percentage of individuals showing one

abnormal behaviour (Table 4) than RO chimpanzees in this age group. However, this result was probably attributable to the small number of RO individuals, where a difference by one individual accounted for a change of 8% (compared to 4% per individual in MGR).

Zoo location was found to have little effect on the behaviour of captive chimpanzees, and higher levels of abnormal behaviours were found at zoos with high numbers of deprived (RO and RA) individuals. However, other variables such as age or sex composition, group stability and area available per individual did not influence the performance of abnormal behaviours. Variables such as age or sex composition, group stability and area available per individual did not influence the performance of abnormal behaviours. The environmental variable that negatively correlated most consistently with abnormal behaviours was the number of feeds that the group received per day. Locations that had a high frequency of feeds, such as Edinburgh Zoo where the group was fed five or more times per day, had lower levels of abnormal behaviours in terms of time spent and frequency of performance. Previous studies have found links between feeding management and abnormal behaviours (Bloomsmith *et al* 1988; Maki & Bloomsmith 1989; Fritz *et al* 1992a; Baker 1997). Bloomsmith and Lambeth (1995) have shown that an unpredictable feeding schedule reduces abnormal behaviours and inactivity in groups of chimpanzees. They found no evidence that a predictable schedule of feeding promoted well-being, as was commonly thought. This is supported by evidence from Edinburgh Zoo, where the group was fed on an unpredictable schedule and showed lower levels of abnormal behaviours, although their normal activity levels were no different to those observed at other locations.

Faecal manipulation was common in all rearing conditions and was thought to be a product of the captive environment caused by the reduction of the amount of time spent performing food-related behaviours. In the wild, this behaviour is rarely seen (Goodall 1986). It is seen in all zoo locations, suggesting that no one management system has been able to eliminate it, and many zoos are keen to reduce this behaviour pattern in their chimpanzee groups. It is interesting to note that locations in which only deprived (RO and RA) individuals are housed had the greatest levels of faecal manipulation. Bloomsmith *et al* (1994) found that coprophagy and faecal smearing were the only abnormal behaviours that occurred regularly in juveniles reared in complex social groups. Coprophagy in great apes has long been regarded as a common abnormal behaviour (Meyer-Holzapfel 1968) and is probably related to reduced feeding time and boredom in captivity. Around 70% of 139 chimpanzees at the Aeromedical Research Colony in the US performed coprophagy (Kollar *et al* 1968). However, coprophagy has been reduced in chimpanzees by providing high-fibre feeds (such as cardboard, stems, celery and straw) as 'wadging' material (Fritz & Fritz 1979; Fritz *et al* 1992a). Baker (1997) found that by providing straw and scattering forage, oral abnormal behaviours (coprophagy, saliva eat, faeces paint, hair pluck, thumb suck, urine drink) of pairs and trios of chimpanzees could be reduced from 4% to 1% of samples and regurgitation and reingestion reduced to less than one third of original levels. In captive gorillas, regurgitation and reingestion is linked to levels and type of feeding, but is more common in hand-reared gorilla infants (both wild-caught and captive-born) than their peers reared without their mother but with conspecifics (Gould & Bres 1986). This was also seen in the present study, with RA individuals having higher occurrences of faecal manipulation than RO or MGR chimpanzees. Such behaviours as faecal ingestion and regurgitation and reingestion are very persistent and difficult to eliminate, despite environmental enrichment (Gould & Bres 1986). Management of these behaviours in great apes should be considered in the long-term, with prevention in infants being more effective than attempts to eliminate this

behaviour later in life. Prevention might be achieved by providing the animals with a stimulating environment and continuous opportunities to obtain high-fibre food sources.

Self-sucking was only observed in three RA adolescent females, at Monkey World and Penscynor. Self-sucking behaviour has been suggested to originate from lack of nursing in bottle-fed infants. Human-reared infants which are fed on demand do not develop self-sucking behaviours (Maki *et al* 1993).

The Monkey World group showed the largest range of abnormal behaviours. It was thought that because the individuals within it had very varied backgrounds, such as photographers' aids and laboratory subjects, many abnormal behaviours had developed prior to resocialisation and had then been introduced into the group. Fritz *et al* (1992b) suggested that some abnormal behaviours pass between individuals by imitation of others, through "pre-cultural" transmission. They found that coprophagy, "finger painting" and depilation are learned from others, whereas motion stereotypies, such as rocking, are not (Fritz 1986). It is likely within the groups studied, and particularly at Monkey World with its high proportion of human-reared infants and juveniles, that abnormal behaviours spread through the group by imitation and thus maintain their presence in the groups' behavioural repertoire.

Animal welfare implications

There are several practical implications of this study relating to this species' welfare and captive management. Abnormal behaviours are often thought to be indicators of poor welfare, which may be expressed in excessive amounts of certain behaviours or abnormal levels of inactivity (Broom 1986). The abnormal behaviours observed in this study are unlikely to be indicators of poor welfare in the present, but rather of past experience of an inappropriate environment. Individuals with deprived backgrounds (RO and RA chimpanzees) performed higher levels of abnormal behaviours even in an enriched environment, whereas others who had always been housed in this enriched environment demonstrated fewer abnormal behaviours at lower frequencies. For example, rocking is a behaviour that is thought to help chimpanzees cope with stress (Spijkerman *et al* 1994). It is thought that, with time, the performance of an abnormal behaviour can become detached from the original stimuli (Mason 1991). On the other hand, as Broom and Johnson (1993) point out, even when abnormal behaviour has become a habit, its presence is still an indicator that the individual is having difficulty coping with its present situation, and the individual's welfare must be poorer than that of an animal demonstrating lower levels of abnormal behaviour. Therefore, the welfare of deprived individuals, especially those that demonstrate abnormal behaviours, is more likely to be compromised than that of 'normal' individuals, even if environmental conditions are good. Management of deprived chimpanzees requires even more consideration and thought than management of captive chimpanzees that have not been subjected to deprivation, as they are more likely to be influenced by physical and social environmental stressors. This is not to argue that 'normal' chimpanzees can tolerate sub-optimal conditions and that environmental improvements should not be a constant aim of their captive management. 'Deprived' individuals may find certain captive situations and experiences stressful whereas 'normal' chimpanzees would find them stimulating or exciting.

The environment is also important in helping to maintain appropriate behaviour in this species. The influence of the environment on deprived individuals probably plays a secondary role in recovery compared to social therapy. As with the studies of Wilson (1982) and Perkins (1992), it was found here that the amount of space available is not necessarily important.

The fact that chimpanzees appear to be able to adapt to maternal separation does not suggest that this process should be advocated. The welfare of infants is compromised when they are removed from their mother. This is illustrated by the fact that abnormal behaviours develop and depression is exhibited. Even in the wild, with the support of their social group, orphans often do not survive the trauma of maternal loss (van Lawick-Goodall 1968; Goodall 1983, 1986). In addition, the ethics of removing infant chimpanzees from their mothers are questionable. Although this is no longer common practice in modern captive chimpanzee management, it does still occur. With the increase in the bushmeat trade, for example, young chimpanzees are often illegally offered for sale as a by-product of the killing of their mothers for human consumption. If youngsters do have to be removed from their mothers as young infants, the human-rearing that they receive should reflect the care the infant would receive from its mother. Constant bodily contact and responsiveness to the infant has been found necessary to prevent the development of self-directed behaviours such as rocking (see Maki *et al* 1993).

Conclusions

As a group, chimpanzees that had experienced social deprivation earlier in their lives showed decreased normal activity levels and increased levels and variety of abnormal behaviours, even though they were living in a social group. When investigated further, it was found that deprived infants showed elevated levels of normal activity and abnormal behaviours, with adults, on the other hand, showing similar levels to 'normal' chimpanzees, suggesting that these effects of human interference are not permanent. However, individuals were idiosyncratic in the degree to which they were affected. Chimpanzees at different locations showed little variation in the behaviours studied, although the number of times per day that the group was fed was found to relate negatively to levels of abnormal behaviours.

Acknowledgements

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