The effects of rearing conditions on grooming and play behaviour in captive chimpanzees

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Abstract

The effects of maternal and peer separation during infancy and juvenescence on adolescent and adult chimpanzee behaviour were studied. The aim was to provide an insight into the social development of the species and to investigate human influence on this process. Forty-three adolescent and adult chimpanzees (Pan troglodytes), from a variety of backgrounds, were studied at five zoos in the UK. Details of play and grooming interactions were recorded. Competence at initiating, maintaining and contributing to play and grooming interactions was assessed. It was predicted that, regardless of their present environment, captive chimpanzees that were reared without their mother would be less competent and complex in these social abilities than mother-reared chimpanzees. Results indicated that the chimpanzees' social skills showed few detrimental effects of maternal separation. Nevertheless, individuals that had been human-reared demonstrated more unsuccessful initiations of social interactions and fewer polyadic grooming interactions than their mother-reared peers. Therefore, rearing background may have only a limited effect on adult chimpanzees' social competence. Adult chimpanzees that were hand-reared or nursery-reared may be exhibiting a recovery of their social skills, or they may be unaffected by their rearing background; alternatively, the effects of rearing may have been masked by more significant factors, such as current management.

Keywords: *animal welfare, chimpanzees, early experience, grooming, play, rearing*

Introduction

The effects of social deprivation on the behaviour of non-human primates have historically received much attention (Harlow 1959; Harlow & Harlow 1962a,b; Davenport & Menzel 1963; Mason 1965; Sackett 1967; Mitchell 1968; Menzel *et al* 1970; Dienske & Griffin 1978). Social deprivation of an individual can be considered to be a lack of a 'normal' upbringing, with 'normal' being that which is observed in the majority of wild individuals. However, most investigations have focused on short-term effects and/or the influence on the individual's ability to produce viable offspring. Earlier studies showed that a deprived background had little influence on activity, abnormal behaviours (Martin 2002) or personality traits (Martin 2005) in resocialised chimpanzees. However, the effects of deprivation may be much more subtle than obvious behavioural changes, and little attention has been given to the influence of early experiences on adult behaviour and to how well these individuals fare in society after resocialisation.

Social skills are required to maintain social order and, although chimpanzee infants have a repertoire of species-specific behaviours, they must learn appropriate social contexts and uses of these communication signals (Goodall 1982). During infancy and juvenescence, wild chimpanzees, under the protection of their mothers, have the opportunity to learn the social behaviours necessary for adult life (van Lawick-Goodall 1973). Within a social group, young chimpanzees learn functional sequences of species-specific gestures, postures and vocalisations (Goodall 1986). It has been demonstrated that infants use teasing as a way of learning social skills by reducing the uncertainty in social relationships and predicting individuals' responses more accurately (Adang 1985, 1986). Cultural differences in social behaviour have been observed between wild and captive chimpanzee groups (summarised by Goodall 1986), revealing the importance of learning in the development of social abilities.

Socially deprived primates have often been described as having inappropriate social skills, but this social incompetence has rarely been systematically tested (but see Anderson & Mason 1974, 1978). Animals reared under restricted conditions may not have had opportunities to learn appropriate social behaviours. Mason (1960) describes their social abilities as being impaired through lack of opportunity to develop the communication skills necessary for social interaction. Mason (1963) also identifies them as poor senders and receivers of social signals and unable to respond appropriately; for example, isolation-reared chimpanzees exhibit little response to being groomed (Mason *et al* 1968). Indeed Miller *et al* (1967) found that rhesus macaques that had been reared in isolation for the first year of life were unable to use the facial expressions of

other monkeys in a cooperative avoidance test, and were also poor at producing appropriate facial expressions. Mitchell *et al* (1979) summarised previous studies to conclude that isolation-reared juvenile and adult monkeys were inadequate in their use of facial expressions and that 'normal' monkeys had difficulty interpreting the behaviours and facial expressions of these deprived individuals. Anderson and Mason (1974) looked at the social complexity of young rhesus macaques and found that those which had been socially deprived showed fewer and less complex polyadic interactions (involving three or more individuals in an interaction) than those reared by their mother with animals of similar age. They also investigated the social strategies used by young rhesus macaques, by observing displacement behaviour at a water bottle (Anderson & Mason 1978). Again, they found that socially experienced macaques were more likely to be involved in complex and triadic interactions than their socially deprived counterparts. They concluded that socially experienced monkeys used more elaborate manoeuvres to influence the behaviour of higher-ranking group members through their responses to other group members. Their results suggest that the development of complex social abilities is dependent on social experience (Anderson & Mason 1978).

Poor social skills have also been described in socially deprived chimpanzees, although not systematically studied. Mason *et al* (1968) suggest that even though play behaviour occurs with the same frequency and with similar patterns in isolation-reared chimpanzees after 5–6 years of living in a social group, it is likely that in the long-term their development of social cue functions is inadequate, when compared to that of wild-born animals. They also describe the grooming behaviour of isolation-reared chimpanzees as being distinguishable from wild-born chimpanzees even after several years of group living. Turner *et al* (1969) looked at the social behaviour of three socially deprived adolescent chimpanzees that had been in isolation for the first three years of life, and compared them to wild-born counterparts. They found that although the socially deprived adolescents played, they never groomed, even in the presence of a 'therapist' (a socialised, often younger, individual which can act as a 'teacher'). During other interactions, socially deprived individuals responded to initiation behaviours, but their initiation behaviours were either ignored or responded to by withdrawal much more frequently than were those of wild-born adolescents. In a case history of a hand-reared, resocialised chimpanzee, Nankivell *et al* (1988) found that the animal had difficulties in interpreting social communication signals.

This study specifically investigated the effects of early life experiences on the social behaviours of play and grooming in adult chimpanzees. The general prediction was that separation from other chimpanzees during early development would lead to a loss of opportunity to learn the appropriate social skills required for chimpanzee society, the impact of which would affect the chimpanzee throughout its life. It was predicted that chimpanzees reared alone (RA) would exhibit deficient social skills for a range of measures of social competence when compared to chimpanzees that had been reared by their mother in a social group (MGR). Individuals that had been separated from their mothers but had been reared with other conspecifics (RO) were expected to show affected social abilities, but affected to a lesser extent than their RA peers. A number of specific predictions were tested. It was predicted that RA chimpanzees would:

(1) have fewer

   a. play partners

   b. grooming partners;

(2) have a lower proportion of polyadic and a higher proportion of dyadic grooming interactions;

(3) take part in less complex grooming interactions (ie interactions with fewer members, which hold less complex roles);

(4) play a less complex role within grooming interactions (ie interact with fewer partners at one time and mainly in a unidirectional manner);

(5) show differences in the initiation of grooming and play behaviour; that is, they would show

   a. less variety in initiating behaviours for both grooming and play interactions

   b. more grooming interactions that commenced with an initiation and fewer with no initiator

   c. longer latencies between initiation behaviours and the start of the behaviour

   d. more repeated initiation behaviours

   e. more unsuccessful initiation behaviours;

(6) show differences in the survivorship and reciprocation of grooming and play behaviour; that is, they would show

   a. shorter latencies between the start and finish of a bout

   b. shorter proportion of time interacting within a bout

   c. shorter proportion of time in mutual reciprocation

   d. lower frequencies of reciprocation.

Methods

Subjects

Forty-three chimpanzees were observed from five different zoos in the UK (Belfast, Chester and Edinburgh Zoos, Penscynor Wildlife Park and Whipsnade Wild Animal Park) between March 1994 and April 1998. Details of the individuals are described in Table 1: 18 individuals had been raised by their mother in a social group (MGR); 12 had been mother-separated during infancy but reared with conspecifics (RO); and 13 had been separated from their mother and conspecifics for a period of time as dependent infants (RA) (although the duration was not always known).

In this study only adolescent and adult group members were observed. This included 15 males and 28 females, of which 17 were categorised as adolescents or young adults (8–15 years) and 26 as prime, mature or old adults (≥16 years). Zoos were selected for their similarity in management styles in order to reduce confounding variables. However, management did vary with location to some extent.

Behavioural observations

A number of behavioural observations were made on aspects of social interaction, namely play and grooming behaviours. Behavioural observations were made between 1000h and 1600h in the spring and autumn of 1996, 1997 and 1998.

Number of play partners

Focal individuals were continuously recorded for 12 15-min sample intervals. During social play interactions, all individuals with which the focal individual interacted were recorded, allowing the frequency and identity of play partners to be noted for each individual over 12 samples. The frequency with which each possible pair of chimpanzees was seen playing was calculated. The resulting data were put into matrices and the Index of Association between all possible play partners was calculated using the following formula (Goodall 1986). The number of play partners for each individual was calculated from the number of associations an animal had that scored ≥5% on the Index of Association.

$$\text{Index of Association} = \left[\frac{\text{A and B together}}{(\text{A without B}) + (\text{B without A}) + (\text{A and B together})} \right] 100\%$$

Number of grooming partners

One-hour observations were made of each chimpanzee group, during which instantaneous scans were made at 3 min intervals. Scans were made at intervals throughout the day regardless of whether grooming behaviour was being performed. At each interval, all grooming interactions were recorded diagrammatically and included the identity of individuals and the direction of the interaction, ie who groomed who. Fifty samples were made of each group, which totalled 1050 scans per individual. Interactions between mother and infant were not recorded when the infant was less than two years of age. The frequency with which each possible pair of chimpanzees was seen grooming was calculated. This was recorded in three different frequency measures for each pair (A and B): (1) the frequency of A grooming B; (2) the frequency of B grooming A; and (3) the frequency of mutual grooming. The data were put into actor matrices and grooming association indices were calculated using the Index of Association, described above for the number of play partners. The number of grooming partners was calculated for each individual by the number of associations they had which were ≥5%.

Number of dyadic and polyadic relationships

The data collected for number of grooming partners were also used to look at the relationship between the partners involved. In dyadic relationships either partner (1 or 2) may perform the grooming, or it may be reciprocated (3):

(1) A→B   (2) B→A   (3) A↔B

In polyadic relationships a variety of combinations of interactions may be seen. An interaction complexity value was assigned to each possible dyad or polyad. This was calculated by summing the number of arrowheads within the diagram (see Anderson & Mason 1974). An individual complexity value was calculated by summing the number of

arrowheads pointing toward and away from the focal individual (with arrows pointing away scoring 2, and arrows pointing toward scoring 1). For example, for the polyad diagram where chimpanzee A grooms chimpanzee B and B grooms chimpanzee C:

A→B→C

Individual B had one arrow pointing toward (score 1) and one arrow pointing away from it (score 2), and so was assigned a total individual complexity score of 3. The role of chimpanzee B in the interaction was one of actor and recipient.

Initiation, survivorship and reciprocation of social behaviour

Ad libitum sampling (Martin & Bateson 1986) was used to record data whenever a grooming or play bout commenced, with or without the presence of visible initiation behaviour. Between 51 h and 63 h of social skill observations were made at each of the five zoos. The criterion of a new bout was defined as when the chimpanzees involved had not been interacting with any other individuals in the 2 min prior to data collection. When a chimpanzee initiated a social interaction, the following details were recorded: the actor and recipient; whether it was play or grooming; the time and type of initiation (as defined in Table 2); and the time between initiation and start of interaction (referred to as 'latency'). If no response was seen within 2 min for both grooming and play bouts, the recording was ceased.

If another initiation behaviour was performed by one of the partners prior to the commencement of the response, then the time of this occurrence, the direction between actors and the type of interaction was recorded. These data provided the latency, the number of abortive signals, and the type of initiation behaviours performed. All initiation behaviours were classified into one of three categories:

(1) Successful and reciprocal — the recipient of the initiation behaviour responds to it within 5 s of it ending;
(2) Successful and non-reciprocal — the actor of the initiation behaviour responds to it within 5 s of it ending;
(3) Unsuccessful — no response is made by either recipient or actor within 5 s of the initiation behaviour ending.

The time at which the interaction, ie play or grooming, commenced was recorded irrespective of whether an initiation behaviour had been performed. The direction between actor and recipient of interaction was also noted, as were all breaks and resumptions of the interaction bout and changes in direction between the partners. From the resulting observations, the total time of the interaction was known, as were the length of time and frequency that each partner contributed to the bout, and the length of time and frequency of mutual reciprocation. Data collected during the first initiation were also collected during any subsequent initiations performed to maintain the bout. Any breaks in the bout longer than 2 min, without repeat initiation behaviours, were deemed the end of the bout and recording ceased.

Statistical analysis

Non-parametric techniques were used as the data did not meet the required assumptions for parametric testing. To

Table 1   Profiles of individual chimpanzees and the number of observations made.

Location	Name	Sex	Age category	Back-ground	No. grooming interactions observed (out of 1050 scans)		No. play partners	No. grooming partners	No. grooming bouts observed			No. play bouts observed
					Dyad	Polyad			With initiator	Without initiator	Total	
Belfast	Helga	F	PMO	RA	113	31	1	5	22	58	80	17
	Elizabeth	F	PMO	RA	75	15	1	5	8	37	45	14
	Andy	M	PMO	MGR	102	32	3	6	28	31	59	35
	Angela	F	YA	MGR	54	25	2	4	5	18	23	15
	Annie	F	YA	MGR	134	31	4	4	12	38	50	11
	Kim	F	YA	MGR	73	8	3	4	25	28	53	28
Edinburgh	Ricky	M	PMO	RA	43	3	1	3	5	10	15	23
	Cindy	F	PMO	RA	35	1	2	4	9	17	26	36
	David	M	PMO	RO	146	5	1	3	8	18	26	11
	Louis	M	PMO	RA	170	8	2	4	14	27	41	19
	Lucy	F	PMO	RO	182	6	0	4	19	23	42	8
	Tom	M	PMO	RO	37	3	0	2	6	12	18	16
	Emma	F	PMO	MGR	86	0	1	4	15	39	54	16
	Lyndsey	F	YA	MGR	50	2	0	2	11	30	41	4
Whipsnade	Daisy	F	PMO	RA	87	1	0	0	13	46	59	6
	Oscar	M	PMO	RA	109	10	3	1	6	18	24	3
	Primrose	F	PMO	RO	48	5	0	0	13	27	40	26
	Bonnie	F	YA	MGR	38	1	2	0	7	22	29	13
	Niki	M	YA	MGR	97	10	4	0	13	29	42	24
	Wally	M	YA	MGR	19	5	3	2	0	11	11	23
Penscynor	Neusi	F	YA	RA	76	0	0	1	17	14	31	3
	Vicki	F	YA	RA	84	0	0	2	29	15	44	6
	Suzi	F	YA	RA	15	0	0	2	8	8	16	0
	Twmi	M	YA	RO	17	0	0	2	7	12	19	3
	Fergus	M	YA	RO	16	0	0	1	5	15	20	4
Chester	Boris	M	PMO	RA	183	100	0	5	15	22	37	11
	Wilson	M	PMO	RO	114	37	1	2	9	25	34	15
	Nicky	M	PMO	RO	97	26	1	4	6	15	21	10
	Friday	M	PMO	RO	185	42	1	3	13	24	37	10
	Meg	F	PMO	RA	75	10	2	1	5	9	14	6
	Kate	F	PMO	RO	157	39	1	4	5	27	32	8
	Cleo	F	PMO	RA	285	87	1	6	8	14	22	2
	Rosie	F	PMO	RO	249	42	0	2	9	26	35	5
	Heidi	F	PMO	RO	180	71	0	4	7	17	24	4
	Halfpenny	F	PMO	MGR	238	74	0	3	8	15	23	8
	Farthing	F	PMO	MGR	173	23	1	2	4	13	17	10
	Mandy	F	PMO	RO	133	25	4	3	6	19	25	16
	Florin	F	YA/PMO	MGR	201	37	0	5	7	24	31	4
	Kan Kan	F	YA	MGR	232	28	2	4	7	11	18	9
	Dylan	F	YA	MGR	89	33	1	2	4	15	19	11
	Sarah	M	YA	MGR	213	66	0	2	4	8	12	7
	Wanda	F	YA	MGR	78	15	6	3	4	9	13	4
	Sally	F	YA	MGR	174	9	6	1	3	9	12	16

Age category:
PMO = Prime, mature and old adults (≥16 years)
YA = Young adults and adolescents (8–15 years)
Background:
MGR = Individuals raised by their mother in a social group
RO = Individuals separated from their mother during infancy but reared with conspecifics
RA = Individuals separated from their mother and conspecifics for a period of time as dependent infants

Table 2   Initiation behaviour definitions.

Grooming initiation behaviours	
Initiation behaviour	**Description**
Present	Sit or stand in front of chosen partner, presenting parts of the body such as the back, flanks or shoulders, often with head bowed (Goodall 1965, 1986, unpublished; van Lawick-Goodall 1968; van Hooff 1973)
Scratch	Scratch vigorously, downwards under one arm, from elbow to belly or vice versa (van Lawick-Goodall 1968; Goodall 1986, unpublished)
Touch	Take the hand of another individual and bring it into contact with own body (van Hooff 1973); also touch arm or hand of partner
Pull	Pull hand or other part of body
Vocal	Whimper, grunt, lip smack
Raspberry	Blow 'raspberry' sound
Other	Idiosyncratic initiation behaviours
Play initiation behaviours	
Initiation behaviour	**Description**
Back present	Sit, facing away and leaning slightly forward; seen in infants toward adults (Goodall 1986)
Bite	Bite partner
Clap	Clap hands together
Finger wrestle	Take hand or foot of partner and make tickling or pulling movements; seen in adults toward infants (van Lawick-Goodall 1968; Goodall 1986)
Grab	Lunge at partner and grab part of their body, eg leg
Head bob	Move head up and down repeatedly (Loizos 1967; Savage & Malick 1977)
Jump	Jump onto another individual
Kick	Kick partner
Kick back	Kick back with one foot while walking past; seen in adult males to infants (van Lawick-Goodall 1968; Goodall 1986)
Pat or tickle	Pat or tickle partner under the chin; seen in adult males to other adults (van Lawick-Goodall 1968)
Play-face	Opened mouth with corners slightly withdrawn; upper teeth remain covered or partly covered and lower teeth are slightly bared (van Lawick-Goodall 1968; Goodall 1986, unpublished)

compare the three rearing conditions the one-tailed *a priori* Jonckheere Test for Ordered Alternatives was used (Siegel & Castellan 1988). For comparisons between males and females and between the two age classes the Mann-Whitney U test for independent samples was used (Siegel & Castellan 1988). For all statistical analyses a significance level of 0.05 was accepted.

Results

A summary of the social interactions observed for each individual can be found in Table 1.

Number of play partners

The number of play partners that an individual had was compared across the three rearing conditions. No significant difference was found, with individuals having on average one play partner. There was no significant difference between males and females and between the two age categories for the number of play partners.

Composition of play interaction

The median value of latencies and frequencies of play initiation behaviours were calculated for each individual. There was no significant difference between rearing conditions for any of the measures of initiation behaviour, with MGR individuals being very similar to RO and RA individuals.

In addition, there was no significant difference between the rearing conditions in the latency and type of repeat initiation behaviour. However, MGR chimpanzees had a higher percentage of successful repeat initiation behaviours (MGR: median = 79.51, inter-quartile range [IQR] = 50.00, n = 14; RO: median = 60.00, IQR = 85.00, n = 9; RA: median = 71.43, IQR = 60.00, n = 11; $J = 233$, $J^* = 1.383$, $P < 0.01$) and a lower percentage of unsuccessful repeat initiation behaviours (MGR: median = 20.49, IQR = 50.00, n = 14; RO: median = 40.00, IQR = 85.00, n = 9; RA: median = 28.57, IQR = 60.00, n = 11; $J = 239$, $J^* = 1.573$, $P < 0.01$).

Age and gender had little or no effect on the measures of play skills. However, male chimpanzees (median = 4, IQR = 3) were found to perform a wider variety of play initiation behaviours than females (median = 2, IQR = 1.75; $U_{[16,25]} = 119$, $P < 0.05$).

Number of grooming partners

The number of grooming partners that an individual had was compared across the three rearing conditions. There was no effect of rearing condition on the number of grooming partners that an individual had. The average number of grooming partners was 3, and ranged from 0 to 6. Prime, mature and old adults (median = 3, IQR = 2, n = 17) had more grooming partners than young adults (median = 2.5, IQR = 2, n = 26; $U_{[16,25]} = 138$, $P < 0.05$).

Structure of grooming interactions

The number of dyadic and polyadic grooming interactions in which each individual was involved was determined, as

was the structure of the interaction and the position (ie actor or recipient) of individuals within all observed dyadic and polyadic grooming interactions. From this information, the following measures were calculated for each individual: percentage of dyadic interactions; percentage of dyadic interactions as actor; percentage of dyadic interactions as recipient; percentage of mutual dyadic interactions; percentage of polyadic interactions; percentage of polyadic interactions as actor; percentage of polyadic interactions as recipient; percentage of mutual polyadic interactions; frequency of being actor; frequency of being recipient; frequency of being mutual; mean interaction complexity; and mean individual complexity.

There was no significant effect of rearing background on any of the measures described above. In addition, the gender of the individual had no effect on performance of dyadic or polyadic grooming interactions.

Prime, mature and old adults were found to hold more grooming interactions in total (median = 151, IQR = 142.25) and were more frequently recipients (median = 51.5, IQR = 52), compared to younger adults (median = 81, IQR = 112; $U_{[16,25]}$ = 120, $P < 0.05$; median = 24, IQR = 21; $U_{[16,25]}$ = 98, $P < 0.01$ respectively). When the different age groups were investigated for differences across rearing conditions it was found that adolescents and young adults did differ for some measures according to rearing condition. MGR adolescents and young adults showed a lower percentage of dyadic interactions and a higher percentage of polyadic interactions compared to their RO and RA peers, with the RO and RA individuals performing dyadic grooming interactions only.

Composition of grooming interactions

It was found that MGR chimpanzees (median = 84.21, IQR = 43.75, n = 17) did perform a higher percentage of successful grooming initiation behaviours compared to RO and RA individuals (RO: median = 50.00, IQR = 30.63, n = 12; RA: median = 58.33, IQR = 34.79, n = 12; J = 373.5, J^* = 2.346, $P < 0.01$). RO and RA chimpanzees (RO: median = 50.00, IQR = 30.62, n = 12; RA: median = 41.67, IQR = 37.80, n = 12) were found to perform more unsuccessful initiation behaviours (MGR: median = 15.79, IQR = 43.75, n = 17; J = 373.5, J^* = 2.346, $P < 0.01$). However, there were no other differences in terms of initiation behaviour.

It was found that rearing condition had no effect on measures of repeat initiation behaviours, latency of grooming bouts, or reciprocation and mutual reciprocation during grooming bouts.

Age and gender had some effect on the performance of grooming interactions. Prime, mature and old adults were found to perform a higher percentage of interactions with successful repeat initiation behaviour (adults: median = 72.73, IQR = 63.33; adolescents: median = 33.33, IQR = 42.86; $U_{[11,24]}$ = 63, $P < 0.01$); they performed a lower percentage of unsuccessful repeat initiation behaviour (adults: median = 27.27, IQR = 63.33; adolescents:

median = 66.67, IQR = 42.86; $U_{[11,24]}$ = 63, $P < 0.01$); and they had longer total grooming bout durations compared to adolescents and young adults (adults: median = 112.00, IQR = 126.88; adolescents: median = 53.00, IQR = 48.50; $U_{[16,25]}$ = 96, $P < 0.01$). Gender had little effect on the measures of grooming bouts. However, female chimpanzees (median = 2, IQR = 1) were found to perform a wider variety of grooming initiation behaviour than males (median = 1, IQR = 1; $U_{[14,27]}$ = 124.5, $P < 0.05$).

Discussion

Rearing condition had little effect on play interactions. Individuals reared without their mothers, both RO and RA chimpanzees, had the same number of play partners, and the composition of their interactions was almost indistinguishable from that of MGR chimpanzees. The only observation that could be attributed to rearing condition was that MGR chimpanzees were more successful at performing repeat initiation behaviours, whereas RA chimpanzees were less successful. As predicted, RO chimpanzees were intermediate. Social deprivation has been shown to affect initiation behaviours in previous studies (Turner *et al* 1969) and this supports evidence from Mason *et al* (1968) that social cue functions may be affected in the long term. The lack of difference in social play between individuals from different rearing conditions is similar to results obtained by Spijkerman *et al* (1995). They found very little difference in play development of young chimpanzees (aged 0–10 years) between those reared in a family group and those reared in a peer group. They also found no difference in bout length, initiation, maintenance, termination and use of play signals between these two groups (Spijkerman *et al* 1996). However, the play of the peer-reared group was more concentrated with fewer breaks, and individuals performed more play-faces during wrestling play, perhaps to reduce the ambiguity of the action, compared with individuals in the family-reared group. In addition, the peer-reared chimpanzees showed less sex differentiation in their social play. Spijkerman *et al* (1996) concluded that peer-reared chimpanzees were as capable of play as their family-reared peers.

The lack of age differences in play behaviour reflects the fact that all of the individuals studied had passed juvenescence. It is well documented that infants and juveniles play more than other age groups (van Lawick-Goodall 1968; Savage & Malick 1977; King *et al* 1980; Hayaki 1985; Goodall 1986; Bloomsmith *et al* 1994; Markus & Croft 1995; Spijkerman *et al* 1995). However, no reliable biological explanation has been found to explain this decrease in play with age (Fagen 1993). Baldwin (1986) suggests that important factors in this decline could relate to several factors: habituation, through the reduction in the novelty of play; punishment, caused by aversive levels of physical effort; and competing responses, such as sexual interaction, infant care, grooming and dominance interactions. Adult chimpanzees were expected to play, as this has been observed in wild adult chimpanzees, with play occurring between adult males, and play being initiated by males in cases of play between male and female adults (Goodall 1986). However, wild adult females have

rarely been observed playing together (Goodall 1986). In this study, play by both males and females was mainly restricted to associations with infants and juveniles. Young adult females were occasionally associated in play, for example Mandy and Kan Kan at Chester Zoo and Kim and Annie at Belfast Zoo.

Grooming interactions within these captive groups appeared to be similar in structure to those observed in wild chimpanzees. In general, chimpanzee grooming interactions commence with or without an initiator, to signal intentions, and are followed by beginning to groom the recipient or presenting to be groomed by the recipient of the initiator. Reciprocation during grooming bouts maintains the grooming session, and if reciprocation does not occur then the bout is usually terminated (Ghiglieri 1984; Goodall 1986). In Kibale, Ghiglieri (1984) found that grooming sessions in wild chimpanzees lasted for an average of 13.42 min, excluding pauses. In Gombe, Goodall (1986) observed longer average grooming sessions. She found that dyadic grooming bouts between adults lasted longer between males (25.9 min) than between males and females (13.5 min), which in turn lasted longer than grooming sessions between adult females (6.3 min). In addition, polyadic grooming sessions lasted much longer than the dyadic sessions described above (35.7 min, 29.9 min and 22.6 min respectively) (Goodall 1986). Grooming sessions at Gombe sometimes lasted up to 2.5 h, and had been observed to involve as many as 10 individuals (van Lawick-Goodall 1968). However, Merrick (1977) estimated that grooming bouts for a group of captive chimpanzees (six wild-born adolescents and young adults) were rarely more than several minutes in length and were generally dyadic and unidirectional (Merrick 1977). In this study, grooming interactions were shorter than those observed for wild chimpanzees, and averaged 4 min in length, with the longest grooming session observed totalling 1 h 15 min. Polyadic interactions (around 12% of an individual's grooming interactions) and grooming interactions involving reciprocation and mutualisation (both around 22% of an individual's grooming interactions) were frequently observed.

In many respects, rearing had a limited effect on grooming interactions, and many of our predictions were not supported. RO and RA individuals did not have fewer grooming partners, and the structures of their grooming interactions did not differ significantly from those of MGR chimpanzees. Within grooming interactions they did not show poor social skills in relation to their maintenance, reciprocation and mutualisation of interactions. Based on the literature regarding rhesus macaques (Mason 1960), it was predicted that RO and RA chimpanzees would have shorter grooming interactions than MGR chimpanzees; however, this was not the case. The structure of RO and RA adolescents' and young adults' grooming interactions was different to that of their MGR peers, in that the former were involved in only dyadic grooming interactions. A similar response to deprivation was observed in a group of 11-month-old rhesus macaques, with socially deprived

individuals performing fewer polyadic interactions than socially experienced peers (Anderson & Mason 1974). Spijkerman *et al* (1997) found that zoo-reared adolescent chimpanzees groomed with their mothers more frequently, but groomed with their peers less frequently than peer-reared chimpanzees groomed with each other. They found that the increased level of social grooming among peer-reared adolescents was not attributable to increased conflict and the resulting need for reconciliation. As with their studies on play behaviour (Spijkerman *et al* 1995, 1996), they found very little effect of peer rearing on grooming behaviour.

Prime, mature and old adult chimpanzees had more grooming interactions than younger individuals, but these were no more complex than the grooming interactions of the younger adults. However, they did appear to be more skilful in their initiation and maintenance of grooming interactions than younger chimpanzees. This would be expected as the use and functional context of social skills have to be learnt (Goodall 1986). Therefore, with age comes experience, improved social abilities and increased motivation to maintain grooming bouts.

From this study it appears that the chimpanzees observed either suffered no detrimental effects of their rearing background or showed behavioural recovery of complex behaviours, such as social skills. A degree of recovery has been seen in other studies on rhesus macaques (Suomi & Harlow 1972; Suomi *et al* 1974) and has been attributed to the presence of 'therapists'. It is possible that the presence of therapists was the cause of social recovery in this study, if it had occurred.

An alternative explanation for the lack of impact of rearing background on play and grooming behaviour is that the effects may have been masked by other factors. The current physical environment and its related housing, husbandry, social competition etc may have been more influential than rearing style. Indeed the environment did produce effects on both play and grooming interactions (Martin 2000); for example, the higher the proportion of RA individuals, the fewer and less complex the play behaviours observed. In addition, play skills were affected by the group size, the area available per animal and the number of feeds per day. Individuals had more play partners in bigger groups, and the variety of successful initiations received increased as the area available increased; as space increased there was more room to play. In smaller spaces play may be inhibited, and there may be a need to give clearer signals as there is less room to escape if there is misinterpretation or escalation to aggression. In groups with a higher frequency of feeds per day, a greater variety of play initiation behaviour was performed. These environmental factors, particularly area available per animal and number of feeds per day, could all bring about social stress in the group if they were at suboptimal levels. However, it appears that the groups adapt their play behaviour to cope with these strains on the social structure. Interestingly, Matevia *et al* (1991) found the opposite effect of area on social play. They found that

levels of social play decreased when a group of adolescent chimpanzees was moved to a larger enclosure. They suggest that this result could be because levels were abnormally high in their previous smaller enclosure (9.26 m³ for 5–6 animals) and that in the larger enclosure they returned to normal levels. No figures were given with which to make a comparison with this study.

The group in which an individual was housed appeared to have a large effect on the structure and composition of grooming interactions (Martin 2000). This was attributed to both the social composition of the group and the physical environment. The physical environment affected grooming interactions, with individual complexity increasing with a decrease in the area available per animal. In addition, stability of the group (measured in years since the last introduction or removal of an individual by unnatural causes), group size, and the area available per animal influenced the composition of grooming interactions. Groups with lower stability took longer to respond to grooming initiation behaviours and were more likely to reciprocate during interactions; smaller groups had more successful and fewer unsuccessful initiation behaviours, and animals with less space were more likely to reciprocate during grooming interactions. Nieuwenhuijsen and de Waal (1982) suggested that grooming might serve to regulate tension in the chimpanzee group at Arnhem Zoo, during crowding in their winter enclosure. They regard grooming as "more subtle and long-term than submissive 'greeting'" (Nieuwenhuijsen and de Waal 1982). From the results discussed above it appears that restrictions in the environment forced the group members to work harder to maintain social grooming interactions, and this prevented or reduced conflicts and stressful situations.

Animal welfare implications

Although chimpanzees that experience maternal separation during infancy are not necessarily permanently affected, this study does not advocate this process. There are also welfare and ethical implications associated with the process of maternal separation during infancy, as discussed in a previous paper (Martin 2005). However, this study demonstrates that, if separation is unavoidable, infants can be successfully resocialised, as assessed by their play and grooming skills. For example, those working to socialise orphaned infants can hope to achieve socially competent individuals. It should be noted that this gaining of social competence cannot be assumed but needs to be nurtured through care-giving that is comparable to maternal care and through relationships with socially competent conspecifics.

Conclusions

Differences in rearing background had little effect on the social skills of chimpanzees as adults in social groups. Although some differences were identified, overall chimpanzees that had been raised with humans or peers showed similar grooming and play skills to those reared by their mothers in social groups. However, one difference that was identified was the initiation of social behaviours. For both play and grooming, MGR individuals appeared to be more successful in their use of initiation behaviours. Furthermore, although deprived individuals used initiation behaviours correctly and with comparable variety to MGR chimpanzees, they differed from MGR chimpanzees in that their grooming relations were more likely to be dyadic. There are several potential reasons for the limited effects of rearing on play and grooming behaviour: deprivation during infancy and juvenescence may have had no effect on behaviour; other factors such as current management and housing may have had a greater impact and masked any effects of rearing; or, behavioural recovery may have occurred. If behavioural recovery of social abilities is possible in this species, it is probably through the presence of other group members.

Acknowledgements

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