

Successful Formation of a Large Chimpanzee Group out of Two Preexisting Subgroups

Michael Seres,^{1*} Filippo Aureli,^{1,2} and Frans B.M. de Waal^{1,3}

¹*Living Links, Yerkes Regional Primate Research Center, Emory University, Atlanta, Georgia*

²*John Moores University, Liverpool, United Kingdom*

³*Psychology Department, Emory University, Atlanta, Georgia*

Descriptions of the formation of relatively large groups of unfamiliar chimpanzees (*Pan troglodytes*) in captivity are scarce in the literature. Nineteen chimpanzees from preexisting subgroups were introduced into a social group at the Yerkes Regional Primate Research Center. The group included two adult males, six adult females along with six dependent infants, and five unrelated juveniles, four of whom had been hand-raised in a nursery unit. Here we provide details on dyadic and multiparty introductions as well as technical details on the indoor/outdoor compound. The introduction process itself took more than 3 weeks, and was completed without major injuries. The introductions combined with 4 years of follow-up data on aggression, grooming, and affiliative behavior confirm that even chimpanzees from an environment that does not promote complex social skills can be formed into a large multimale–multifemale group. During the introductions, low rates of agonistic behavior among adult females were offset by high rates of affiliative behavior. The two adult males, however, showed contact aggression during the first 10 minutes, after which such behavior virtually disappeared, whereas affiliative behavior increased. Three months after their first introduction, the two males reversed dominance ranks within the group, and hierarchical stability has been maintained since. During the 4-year postintroduitory period, grooming rates slightly decreased, but group cohesion was maintained. The frequency of aggression among all adults, including the males, increased during the 4-year period, but aggression was generally of low intensity after the first year. Zoo Biol 20:501–515, 2001. © 2002 Wiley-Liss, Inc.

Contract grant sponsor: National Institutes of Health; Contract grant number RO1-RR09797; Contract grant sponsor: NCRR/NIH Basegrant of the Yerkes Regional Primate Research Center; Contract grant number: RR00165.

*Correspondence to: Michael Seres, Max-Planck Institute for Evolutionary Anthropology, 22 Inselstrasse, D-04103 Leipzig, Germany. E-mail: mseres@eva.mpg.de

Received for publication May 8, 2001; Accepted August 10, 2001.

Key words: chimpanzees; *Pan troglodytes*; group formation; introduction; aggression; captive; grooming

INTRODUCTION

The reduced use of chimpanzees in biomedical research, and the high production of young chimpanzees in research breeding programs and at zoos, have together created a situation in which these apes have become “surplus” animals in need of alternative housing and care. Breeding is now largely on hold, and institutions are seeking to establish naturalistic social groups in “sanctuaries.” Calls for the establishment of naturalistic captive groups go back to Garner [1896], and specific suggestions for such groupings were already made by Kortlandt [1960, 1966] and Reynolds and Reynolds [1965].

A handful of zoos and research institutions have successfully established (or resocialized) large group of chimpanzees [Mottershead, 1959; van Hooff, 1973; Pfeiffer and Koebner, 1978; Fritz and Fritz, 1979; Adang et al., 1987; Noon, 1991; McDonald, 1994; Alford et al., 1995]. Such groups have proven to be draws for the public, are an optimal educational resource, and serve the study of naturalistic social behavior and communication at a level of detail unimaginable in the field [Kollar et al., 1968; van Hooff, 1973; de Waal et al., 1980; de Waal, 1982; Pereira et al., 1989; Baker and Smuts, 1994; Alford et al., 1995; Pruett and McGrew, 2001]. In our definition, a naturalistic social group of chimpanzees includes multiple adult males and multiple adult females with offspring, with a minimum total of 15 apes. Not all zoos and research institutes want such large groups, or have enough individuals to establish them, but there is also a general reluctance to choose this direction out of fear of excessive aggression and injuries among the chimpanzees. Without trivializing these risks, because they are real and serious both in captivity and in the field [de Waal, 1986; Goodall, 1986a; Nishida et al., 1995; Bloomsmith et al., 1996; Wrangham and Peterson, 1996], the purpose of this study is to describe an introduction process in which an attempt was made to reduce the risk through individualized management (i.e., management based on careful consideration of each individual’s personality, social tendencies, and needs). For a recent review of group introductions, see Fritz and Howell [2001].

In the end, the benefits in terms of psychological well-being and social activity seem to outweigh the potential costs of occasional injury inherent in chimpanzee group-life [de Waal, 1992]. Although the management of large groups is not unproblematic, some zoos and research institutions now have decades of experience and a set of management guidelines has been developed [e.g., Riddle et al., 1982; Fulk and Garland, 1992; Bloomsmith and Baker, 2001]. It is impossible to create a stimulating, naturalistic environment for chimpanzees without accepting some degree of stress in their lives—on the contrary, both the ups and the downs of social life are part of environmental enrichment, and both occur under field conditions [Sackett, 1991].

Past successful large-group formations have been documented in detail, such as the one at Burgers Zoo in Arnhem, the Netherlands [Adang et al., 1987; van Hooff, 1973]. In 1971, a group of chimpanzees was formed out of 18 individuals including 5 males and 13 females (12 adults and 6 adolescents). Except for one individual, most apes had previous social experience. Before releasing all individuals together at once (no dyadic introductory methods were used), the apes were lightly sedated by administering 75 mg chlordiazepoxide (Librium) to lower their

initial excitement and avoid aggression [van Hooff, 1973]. The sedation did not produce the desired effect, however, and two individuals had to be removed. Tepel, a female, was later reintroduced, but a young female, Wendy, was permanently ostracized [van Hooff, 1973]. Two fatalities occurred later, when more individuals were added to the core group. Eventually, the level of aggression declined, and affiliative interactions increased over the years [Nieuwenhuijsen and de Waal, 1982]. By the end of 1984, the colony counted 30 individuals, and the group is still together now, almost 30 years later. The Arnhem group is considered to have had the highest natural reproduction (i.e., reproduction without artificial intervention, such as removal of newborns) of any captive chimpanzee colony in the world [Adang et al., 1987; de Waal, 1998].

Multiple group formations took place at the University of Texas Science Park in Bastrop, Texas, where several multimale/multifemale social groups have been maintained during a 16-year period [Alford et al., 1995]. A total of 397 introductions took place over the years using methods of visual, dyadic introductions allowing individuals to meet each other in every possible combination before they were moved to a compound for the final group introduction. In the eight established, long-term groups each containing between 5 and 11 adults, a total of 98 male–male, 215 male–female, and 284 female–female introductions took place. Fourteen percent of the total male wounding during introductions required surgical treatment [Alford et al., 1995].

Another carefully documented introduction took place at the Detroit Zoo, in 1989, involving 11 individuals, and the introduction process took 8 months [McDonald, 1994]. A stepwise dyadic introductory method was used to great effect. Group members came from various institutes and their background varied from wild-caught to hand-reared as well as mother-reared individuals, ranging in age from infants to adults. A total of 30 pairs went through 70, often repeated, introductions. The highest rates of aggression occurred between two adult males, who had peaceably lived together for years at the zoo. Serious aggression between them occurred after the first introductions to females, and became so problematic that the two males had to be separated for 2 months before the whole group was finally put together [McDonald, 1994].

Among adult females at the Detroit Zoo, dominance relationships did not form without contest, nor did they stabilize quickly. The females showed 1) a high level of spontaneous, unprovoked fights; 2) frequent reconciliations after fights; and 3) opportunistically changing coalitions [Baker and Smuts, 1994]. Dominance interactions during dyadic introductions did not predict dominance rank once the entire group was put together, suggesting that individual characteristics, such as physical strength, age, and personality were not the sole determinants of rank. Several females made sustained efforts to improve status after initial interaction [Baker, 1992; and personal communication]. Baker and Smuts [1994] concluded from their observations that female chimpanzees can be as politically competitive as males.

Here we report on the formation of a 19-member group previously housed in two subgroups in smaller indoor–outdoor cages at the Yerkes Main Station (YMS). There were two adult males, six adult females along with six dependent infants and juveniles aged from 51 days up to 4 years. Of five additional juveniles (Table 1), one was mother-reared (but joined the group without her mother), and four had been hand-raised in the YMS's nursery. These four juveniles had lived together in group A for a little more than a year before departure to the Field Station, and were still gaining social skills. All adults had previous experience in small social set-

TABLE 1. Individuals involved in the colony establishment and their age at the time of first introduction (rounded off in years for individuals older than 5 years, given in months for those younger)

Individual	Sex	Age at introduction	Orig. subgroup
Amos (Am)	M	12 y	B
Phineas (Ph)	M	28 y	A
Ericka (Ek) & Virginia (Vg)	F & F	Ek: 19 y/Vg: 29 mo	A
Tai (Ta) & Daisey (Ds)	F & F	Ta: 28 y/Ds: 47 mo	A
Barbi (Ba) & Sean (Se)	F & M	Ba: 17 y/Se: 18 mo	B
Waga (Wa) & Sallie (Sa)	F & F	Wa: 12 y/Sa: 17 mo	B
Cynthia (Cy) & Reid (Rd)	F & M	Cy: 13 y/Rd: 4 mo	A
Vivienne (Vv) & Steward (St)	F & M	Vv: 19 y/St: 2 mo	B
Sierra (Sr)	F	48 mo	A (and nursery)
Pollyanna (Pl)	F	55 mo	A
Chip (Cp)	M	54 mo	A (and nursery)
Magnum (Mg)	M	48 mo	A (and nursery)
Barney (By)	M	46 mo	A (and nursery)

The table also gives the individuals' two-letter codes, their sex, and the original subgroup (A or B) from which they came.

tings, but none of them had ever lived in the sort of large social group that we were about to form.

The purpose of this group formation was to 1) form a relatively large, socially complex multimale, multifemale group and to study their social behavior longitudinally; and 2) provide this group with a much larger enclosure, about 13 times the floor size of their original YMS's cage-size. The new enclosure was equipped with many toys, ropes, hammocks, and climbing structures, and its outdoor section was covered with grass and weeds.

MATERIALS AND METHODS

Environment

In 1993, an 880 m² indoor–outdoor compound was constructed at the Field Station of the Yerkes Regional Primate Research Center to house up to 25 chimpanzees. The compound consisted of a 525 m² outdoor enclosure, five indoor dens each measuring 3.5 × 3.6 × 2.9 m, and an additional 10 indoor/outdoor “wing section” (runs) that could be interconnected (Fig. 1). The latter section would later become available for another, smaller group of chimpanzees.

Subjects

The first three-members of subgroup A (Phineas, an adult male, Ericka, an adult female, and her offspring Virginia) arrived from the YMS on September 3, 1993. Their preexisting group consisted of one adult male, three adult females and their offspring, and seven unrelated juveniles (six of which were nursery reared).

Other members of the same group arrived within a week: Tai, her daughter Daisey, and Pollyanna, a 4½-year-old juvenile female with no immediate relatives. Members of subgroup B arrived separately in the same week: Amos, a young adult male, and Barbi and Waga, two adult females and their offspring. Members of subgroup B belonged to a preexisting group that consisted of two adult males, 6 adult females, and 2 offspring.

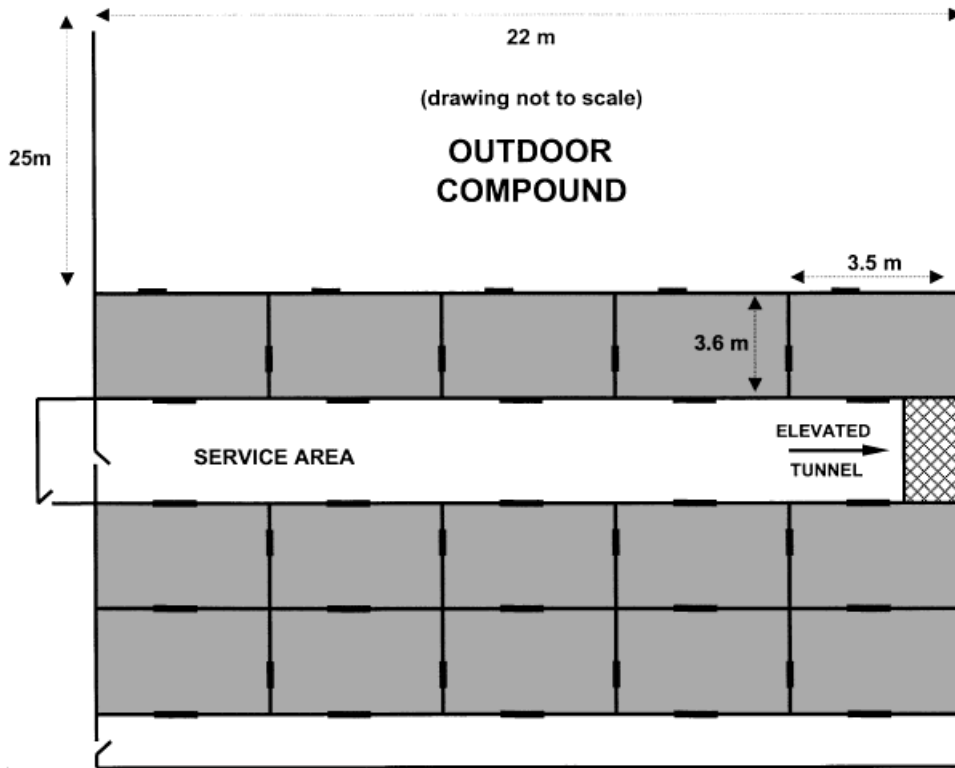


Fig. 1. The building in which the introductions took place had 15 interconnected cages. Dyadic introductions usually involved two or three cages. Release into the large outdoor compound occurred only after establishment of the entire group through carefully monitored procedures.

Among the selected individuals left behind at the YMS were two adult females, Cynthia from group A and Vivienne from group B, their infants, as well as four nursery-reared juveniles, also from group A. They were transferred to the Field Station about 2 months later. The reason for the delay was that both Cynthia and Vivienne had newborns. In fact, Vivienne's departure from the YMS was delayed because she gave birth to her new son, Steward, 5 days after the first chimpanzees arrived at the Field Station. Cynthia's son, Reid, was only 2 months old. The four nursery-reared juveniles—three males and one female—had already lived together with group A since June 1992 at the YMS. Another adult male, Roger, the dominant male over Amos in the original group B, did not accompany his group to the Field Station. Phineas, the dominant male of group A, sired Amos, now in group B, yet the two males most likely had no knowledge of this connection, never having seen each other since Amos was a juvenile.

During the formation of the eventual group we obviously sought to avoid major injuries. Consequently, we reduced visual access before actual physical introductions on the assumption that such access might lead to a building up of antagonism between the members of the different subgroups through bluff displays and other intimidations. The decision about which individuals should take part in dyadic introductions was based on the level of familiarity, with all "unfamiliar" adults (i.e., members of different subgroups) to be introduced to one another. All introductions were

observed in detail and recorded by spoken account. We also kept a diary of daily events. Observations were carefully evaluated before we proceeded to the next step. We often carried out unplanned immediate decisions based on our judgment of the individual chimpanzees' reactions to each other.

Data Collection

During the entire introduction period, data were collected by the first two authors, both of whom had years of experience with chimpanzee behavior. Hand-held audio-recorders and stopwatches were used to record narratives of all social interactions during dyadic introductions, such as affiliative contacts (e.g., patting, embrace, grooming, play, kiss, hand/finger to mouth, mount, genital touch) as well as semiagonistic and agonistic behavior (e.g., bluff, sway, swagger, chase, grab, bark, grunt, scream, bite). Data collection on the entire social group, in the years subsequent to the introduction procedure, included 5-minute scan samples of state behaviors (e.g., grooming) and point-events such as mounting, kissing, embracing, submissive greeting (i.e., pant-grunting), bluff displays, hooting, and aggression. These data were recorded during 90-minute observation sessions on a Tandy-102 portable computer with a program that provided a time statement, supplemented with audio-recorded narratives for events too fast to follow with the keyboard method. The ethogram is a modification of detailed behavioral accounts by de Waal and van Hooff [van Hooff, 1974; de Waal and van Hooff, 1981].

RESULTS

Phase 1: Visual Introductions

While completing transportation, we housed all arriving chimpanzees indoors with subgroup members at the new compound; the two subgroups were housed next to each other, so they could hear but not see one another. We began the visual introduction procedure on the 14th of September. Groups A and B were allowed to face each other twice, on 2 consecutive days. On the first day, we let them to see each other for 80 minutes. As members of group B slowly moved through the elevated tunnel into cages at the opposite side, they began to see group A members for the first time. The two adult males showed piloerection and performed undirected silent bluffs, but their excitement slowly diminished. Amos calmed down first and remained in the back, while Phineas continued to sexually invite (i.e., penis presentation) females of the other group. He also continued bluffing around occasionally.

The following day we started the visual introduction again, this time for 3 hours and witnessed very little agonism between the two groups. The males watched some of the females. The highest-ranking female of group A, Ericka, maintained eye contact with the adult male of group B, Amos; she even reached out to Amos with her hand open, while others engaged in within-group grooming. Judging that both groups were calm, and individuals still showed curiosity toward one another, we decided to proceed with dyadic introductions before habituation would set in, or worse, some higher degree of intergroup antagonism could develop.

Phase 2: Dyadic Introductions

All adult members of different subgroups that were initially present at the Field Station were introduced to each other during dyadic introductions. We began with

the first dyadic, physical introduction on September 16th. After visual introduction between strangers, we allowed initial physical contact in dyadic settings through a 10-cm gap by cracking open a door between interconnecting cages. Various combinations of dyadic introduction required various lengths of introductory time based on the dyads' initial reactions to each other before we allowed full physical access by opening the interconnecting door. Depending on the individuals' behavior, we had sometimes two or three interconnecting cages open for physical interaction. We allowed individuals to be fully together for various lengths of time until we saw that either affiliative behavior increased or that they lost interest in each other. We usually witnessed signs of immediate submission by one of the two adults, and seldom aggression. At the end of each session, we separated and returned each individual to their original group. Overnight we kept subgroups A and B separate and out of each other's sight.

During dyadic introductions, all other chimpanzees were kept out of visual range to prevent them from providing visual or auditory support in case a conflict would break out. Verbal commands to delegate individuals from run to run were brief and consistent, designed to not betray any human side-taking in the introductions because chimpanzees appear to be sensitive to such attitudes. All adults were introduced once to adult members of the other subgroup. Only with the two adult males, we repeated the dyadic introduction three times on different days.

Table 2 shows a brief summary of dyadic introductions between adults (a female's offspring was never separated from her during any phase of the introduction). We categorized agonistic behavior into three different levels: *mild*, such as bluff displays, hooting, swagger, stampot, banging on wall or door, piloerection, arm-threat; *medium*, such as bark, charge, push, pull, and punch. *Severe* included serious aggression that contained fierce/sustained physical contacts such as hit, trample, and bite, sometimes resulting in injury. Formal dominance [cf. de Waal, 1998] was established if a minimum of two submissive pant-grunts were directed by one individual toward the other. In the *contact* category, we included all affiliative contacts except for grooming. *Allogrooming*, either one-sided or mutual, was considered whenever it occurred for at least 5 seconds. Figure 2a shows that the frequency of agonistic interaction in female–female and female–male dyadic introductions was relatively low, that grooming remained stable during the three 10-minute blocks of the dyadic introduction, that other affiliative interaction was high in the first 10-minutes but then decreased, and that dominance–subordination interactions were most typical of the first 10 minutes. Figure 2b shows that agonistic behavior was relatively high in the first 10 minutes during male–male introductions, but virtually disappeared in the third 10-minute block, whereas grooming and other affiliative behavior remained stable or increased over time.

Phase 3: Group Introductions

On September 27th, we introduced the four adult females of different original groups, with their offspring, providing four interconnecting runs to increase space. We kept the two adult males out of sight. During this phase of introduction, Pollyanna, the juvenile female without relatives, was introduced to group B females and their infants for the first time with no hostility toward her. Ericka, group A's top-ranking female, attacked and slightly bit the foot of Waga, an adult female of group B, but 27 minutes later they reconciled, and Ericka groomed Waga. Despite the occasional charg-

TABLE 2. Dyadic physical introductions (for individual codes, see Table 1), and the behavioral frequencies observed for three intensities of agonistic behavior, dominance outcome, grooming initiatives, and other affiliative contacts

Date	Individuals	Sex	Agonism			Dominant	Contact	Groom	Description
			Mild	Medium	Severe				
16 Sept	Ba, Ta	FF	4	2	0	Ta	24	0	Ta armswayed at Ba, who was submissive
17 Sept	Am, Ph	MM(1)	3	11	1	Ph	14	8	Ph bit Am, but then they reconciled and groomed
17 Sept	Ek, Wa	FF	0	3	0	Ek	15	2	Wa screamed and then panted to Ek. Ek groomed Wa
20 Sept	Am, Ph	MM(2)	4	5	0	—	20	17	Embraced each other, and then extensive grooming
21 Sept	Ba, Ek	FF	0	1	0	Ek	19	28	Ek bluffed at Ba, she screamed then they groomed
22 Sept	Am, Ta	MF	3	1	0	—	9	5	Am embraced and kissed Ta then groomed her
22 Sept	Ph, Wa	MF	5	4	0	Ph	9	0	Ph mounted Wa several times, Wa was swollen
23 Sept	Am, Ek	MF	1	2	0	Am	11	15	Am bluffed at Ek, then they groomed
23 Sept	Ph, Ba	MF	1	3	1	Ph	26	2	Ba was submissive, but Ph became aggressively excited
24 Sept	Am, Ph	MM(3)	5	4	0	Ph	14	16	Am did most of the grooming, Ph groomed a little
29 Oct	Cy, Vv	FF	0	0	0	Cy	0	0	Vv was submissive; Cy seemed uninterested

F, female; M, male; Dominant, individual acting dominant over his/her introduced partner; Contact includes touch, embrace, kiss, finger/hand in mouth, and genital touching. The one male–male introduction was repeated three times (i.e., MM 1, 2, and 3).

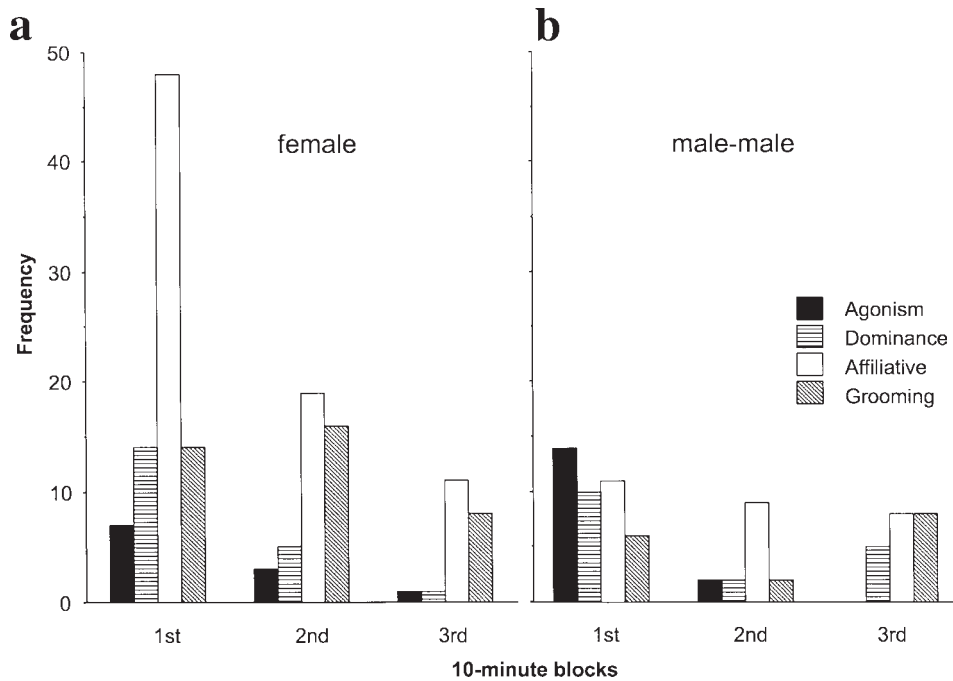


Fig. 2. The graph shows the frequency of four social interaction types (i.e., agonistic interaction, dominance interaction, affiliative contact, and allogrooming) across the first three 10-minute time blocks of dyadic introductions between unfamiliar chimpanzees. **a:** Combined frequencies for all female–female and male–female dyadic introductions show that agonism was rare or absent, and that the introductions were mostly characterized by affiliative contact and grooming. **b:** Two adult males were dyadically introduced on three separate occasions. The graph shows that agonism tended to occur at first, but that the later part of the introductions were characterized by affiliation and grooming.

ing displays by the two males in the back, all of the adult females remained calm during the 1.5-hour introductory period, occasionally embracing each others' offspring, but mainly avoiding physical contact. Tai, the oldest group A female, remained inactive, but Waga and Barbi from group B submissively pant-grunted to Ericka. Splitting the females up and returning them to their male companions went without a problem.

On September 29th, we allowed all adult chimpanzees to come together. We first reunited the two males, then shortly afterward, in separate cages, all four females and the young (including Pollyanna). Finally, we let the two males join the females and young. This time we connected 10 runs together: five interconnected runs indoors, and five outdoors. We observed multiple grooming interactions among the females, and both males groomed females (particularly Ericka), after which a variety of affiliative and play behaviors occurred alternated by occasional bluff displays by both females and males. The females pant-grunted to both males. Play interactions among juveniles, as well as juveniles playing with unrelated adult females, was common. No serious aggressive interactions, certainly no injuries, were observed.

Phineas of group A spent most of his time with females of group B, whereas Ericka of group A spent most of her time grooming Amos of group B. We let the entire group stay together for 3 hours and then separated them again into the original

subgroups. We repeated this introduction the next day. Forty minutes into this introduction, we saw the two adult males groom each other for the very first time in the group context. Three hours later, we separated the new group differently than before: we let the two males sleep together apart from the females, and all adult females and their offspring spent the night together.

Then finally, the next day, 13 days after the first dyadic introduction, we opened the guillotine doors leading to the outside, and let all individuals out into the large enclosure. Because none of these chimpanzees had been exposed to a grassy enclosure before, they were fearful, and had to be encouraged to leave the building. Considerable amounts of food (fruit, biscuits) and plenty of browse material were distributed to ease fear in the new environment. At night, we separated them to sleep with previously familiar companions. It took the apes more than 2 weeks to fully explore (i.e., walk in the grass) and familiarize themselves with their outdoor area after the first release.

Phase 4: Adding Two More Adults

On October 29th, the last two adult females, Cynthia from group A and Vivienne from group B, and their newborn infants, were introduced to each other (Table 2) and then to the four nursery-reared juveniles originally from group A. This was the first time these juveniles were included in the introductory process. All other chimpanzees were locked into their outdoor enclosure to avoid any possible interference.

On the same day, we reintroduced first Vivienne and her infant to her original group B female members, and then Cynthia and her son, and the nursery-reared juveniles to their original group A female members. The two adult males were at this time locked out in the outdoor compound. Again, we kept the two original subgroups separated overnight. The next day, the reunification of Cynthia and Vivienne along with their offspring and the four juveniles took place in five interconnected runs. All previously introduced females and their offspring were allowed inside, and for the first time, all females from groups A and B were together. The two adult males remained locked outside again. The alpha female of group A, Ericka, was immediately dominant over all females. Minor squabbles and avoidance among other females were occasionally seen. We repeated this part of the introduction again the next day, using the indoor and outdoor runs.

On November 2nd, all females and juveniles were released together with the two adult males in the outdoor compound. The four nursery-reared juveniles were immediately submissive to both males, whereas Pollyanna, the 4-year-old independent juvenile of group A, was protected by Ericka whenever necessary.

Phase 5: After Group Establishment

Two major events took place in the months after the aforementioned introductions were completed while the entire group lived together in the indoor–outdoor compound.

First, the older of the two adult males, Phineas, lost his dominance over Amos, his son. Phineas had gained dominance during the first dyadic introduction over Amos on the 17th of September, 1993, which dominance he maintained until the 5th of January, 1994, when he first showed submissive pant-grunts to Amos. Phineas has been the beta male in the group since. The first observed sign of the takeover was a dispute involving the dominant female, Ericka. Ericka used to live in Phineas' group (group A) at YMS, in which she was the dominant female. As reflected in received

pant-grunting and performed display behavior, Ericka also became the dominant female, without contest, over all other females in the newly assembled group and maintains this rank currently. From the beginning, this female seemed to prefer the younger adult male, Amos. In the group context, Phineas three times attacked and tried to overpower the physically stronger (i.e., heavier) but socially less experienced Amos.

On the first of these occasions, November 4th, Phineas attacked Amos, when the latter tried to sexually mount Ericka. Ericka exhibited maximum anogenital swelling, and had solicited Amos for copulation. Phineas knocked Amos over, and Ericka also turned against Amos. She provided only vocal support to Phineas, however. Amos counterattacked and bit Phineas, causing a bleeding wound on his rear. The two males did not reconcile for at least 3 hours.

The second time, a day later, Phineas viciously attacked Amos for the very same reason, but Amos again proved stronger. He pinned Phineas to the ground, slightly biting him on his back and rear. Both males were slightly bleeding, but none of their wounds were serious. Phineas did not give up and attacked, but only hit Amos repeatedly, until he was visibly exhausted. Some females, including Ericka, barked against Phineas. Ericka then approached Amos and inspected his wounds, kissed him, and groomed him. The females ignored Phineas. Less than 30 minutes later, Amos initiated reconciliation with his opponent, walking up to him on the climber, and the two males embraced, after which Phineas vigorously groomed Amos. They engaged in mutual grooming for a long time, while they repeatedly panted to each other. The two males avoided confrontation and both were relaxed for the next 17 days. They engaged in mutual grooming on numerous occasions, and affiliative interactions were on the rise.

On November 22nd, however, Phineas attacked Amos for a third time, again in a dispute over females. Other than placing a few bites on each other, nothing serious happened, and grooming followed again. No further fights between them were observed, although Phineas had a new puncture wound on his left palm on January 3rd. This was probably his last injury caused by Amos. On January 5th, Phineas began to bow and pant-grunt to Amos, a visible and audible sign of formal submission [de Waal, 1982; Noë et al., 1980]. Not a single, not even a minor physical fight has been observed between them in the first 5 years of colony establishment.

The second major social development was that Amos, already the group's alpha male, began to single out one of the juvenile nursery-reared males, Barney, as a target of aggression. From the beginning, this young male showed inexperience in dealing with Amos. We had the impression that he did not know hierarchical boundaries, and triggered negative reactions by invading Amos' individual space at inopportune moments. Social rejection and other forms of exclusion are well documented in captivity and in the field [van Hooff, 1973; Goodall, 1986b; de Waal, 1986; Adang et al., 1987; Nishida et al., 1995]. Amos attacked Barney twice, biting him on two occasions within a 20-day period in March 1994, so that we felt the need to remove Barney from the group. He is now back at the YMS, where another group has accepted him.

Phase 6: Long-Term Data

We began with systematic data collection on this newly formed group on the 4th of October, 1993; the data collection continues to this day. Figures 3 and 4 provide grooming and aggression data until the end of 1996, using over 400 hours of observation. Figure 3a shows that grooming decreased somewhat over time, but remained an active component of daily social life, whereas Figure 3b shows that ag-

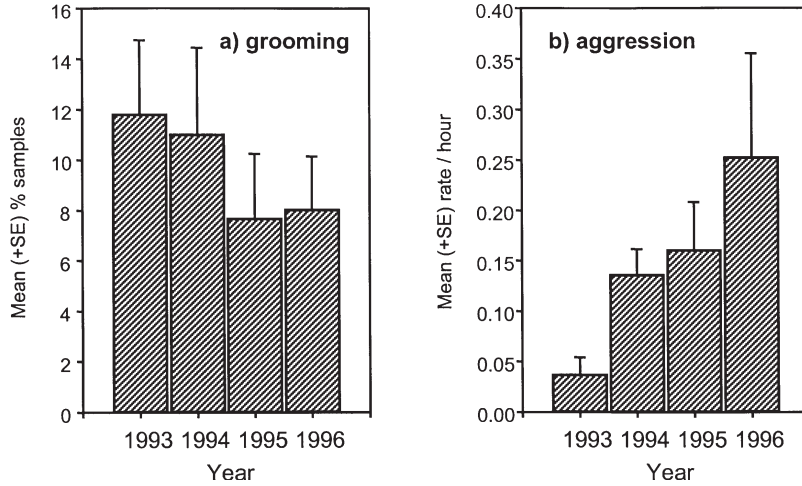


Fig. 3. Mean value (\pm SEM) of grooming and aggressive behavior per adult toward any group member (excluding offspring younger than 3 years) during the 4 years since the introduction, which took place in 1993.

gression started with a low frequency, but gradually increased, reaching far higher levels than in the first year. However, the intensity of aggression (percentage of agonistic interactions that includes severe physical contact) dropped dramatically after 1993, and remained low thereafter (Fig. 4). See Baker et al. [2000] for injury data on this and other chimpanzee groups at Yerkes.

DISCUSSION

Forming a relatively large group of chimpanzees in captivity is not only desirable for enrichment purposes: it is eminently feasible. The methods described here

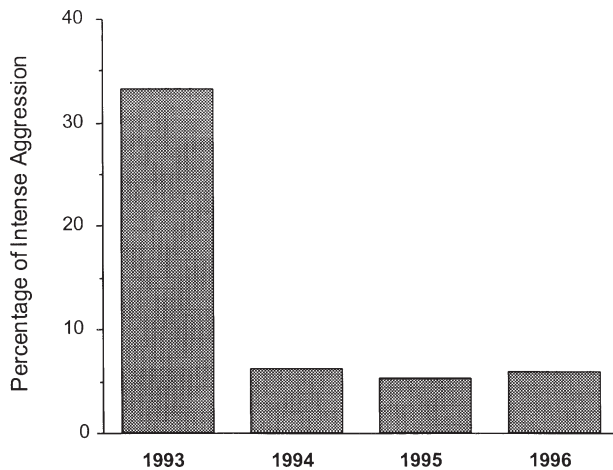


Fig. 4. Percentage of aggressive incidents directed by adults toward any group member that include severe physical contact such as sustained hitting, trampling, or biting.

may provide guidance for future projects, such as group formations expected in the coming years when chimpanzee sanctuaries are to be established. The positive outcome of our introduction should encourage institutes to form groups using individually or pair-kept chimpanzees. With the methods described here, it may be possible to assemble large groups. Obviously, there is never a guarantee of success (experience shows that some individuals can never be integrated in a given group), yet there is certainly no reason to avoid forming such large groups.

The introduction method followed was gradual yet not slow: the entire process took approximately 6 weeks from first introduction to formation of the entire group. It could have been done faster, such as within 1 month, had all chimpanzees been available at the same location at the same time. In contrast to the Arnhem introductions [van Hooff, 1973], no sedation was used, and in contrast to the Detroit introductions [McDonald, 1994], no enduring tensions between adult females ensued. In fact, the female introductions went remarkably smoothly [similar to reports by Alford et al., 1995; Brent, 1997], perhaps because it was obvious from the outset that Ericka would be the alpha female.

Some previous introductions, such as the one at the Detroit Zoo, may have run into trouble because of clashing individual "ambitions," hence lack of submission, between particular dominance-oriented individuals. Such hierarchical uncertainties may be preventable by careful data collection on the social configuration of the pre-existing subgroups to be used, and personality measurements of the chimpanzees to be assembled. Preformation screening was not used in our project, however, nor was this done at the Detroit Zoo, making the different degree of difficulty encountered during the introductions in Detroit versus Yerkes perhaps largely a matter of chance. We believe, however, that this chance factor can be eliminated or reduced with appropriate preformation screening techniques that we are currently developing. They include an estimate of compatibility between individuals based on previous experience with them in a social setting.

In addition, let us point out that one important difference between the present introduction and the one at Detroit Zoo is the presence of infants and juveniles, which accompanied adult females during the introductions. We were struck by the lack of problems this caused. Could the smoothness of female introductions have been partly because of this presence? Young chimpanzees may provide relief from tensions by attracting one adult's attention away from the other adult, and youngsters may bring a welcome element of relaxation, given that they quickly move toward establishing play relations. Apart from this appeasing effect, females carrying infants are probably less likely to engage in protracted dominance battles because the presence of an infant changes their risk assessment. Chimpanzees are known to be occasionally infanticidal in the field [e.g., Goodall, 1986a], hence involving infants also carries risks, and the attitudes of unfamiliar individuals toward infants should be closely monitored.

It is important to have personnel involved who know the animals intimately, and are extensively familiar with chimpanzee behavior. For example, to judge whether an injurious fight has reached an unacceptable level, which calls for the removal and veterinary treatment of one or several of the combatants, requires that one is able to judge the fight's severity relative to other fights. It also requires that one monitors the degree of relationship repair (e.g., "reconciliation") that follows the fight. A reconciled fight may be the only way for certain combinations of individuals to estab-

lish a relationship, whereas a milder but unreconciled fight may hint at lasting incompatibility. Removal of injured individuals thus needs to be weighed against the benefits of giving them a chance to “work things out.” These are complex decisions requiring the input of both behavioral scientists and veterinarians.

Finally, the pattern of dramatically increased aggression rates during the 4 years after group formation fits predictions from the Relational Model of conflict resolution, according to which the reparability of relationships (probably depending on their quality and security) will reduce the risks associated with aggressive confrontation, which in turn may facilitate the expression of aggression [de Waal, 2000; Cords and Aureli, 2000]. This seems counterintuitive, but the observed rise of aggression paired with decreased aggression intensity fits this pattern. Future analyses will test another prediction, namely, that the conciliatory tendency in the colony increased over the years.

CONCLUSIONS

1. Unfamiliar adult chimpanzees can be safely introduced to each other in a confined space (permitting intervention) when the introduction is conducted gradually.
2. We were successful with dyadic introductions of adults (without excluding dependent offspring) preceded by visual introduction, and supervised tactile introduction through a partially opened door, or mesh.
3. Once established the colony went through hierarchical rearrangement and experienced increased aggression rates yet decreasing aggression intensity.

ACKNOWLEDGMENTS

This research was supported by a grant from the National Institutes of Health to F.dW. (number RO1-RR099797). We thank the Yerkes' Veterinary Staff and the Field Station Care Staff for their support during the introduction process. The Yerkes Primate Center is fully accredited by the International Association for Assessment and Accreditation of Laboratory Animal Care.

REFERENCES

- Adang OMJ, Wensing JAB, van Hooff JARAM. 1987. The Arnhem Zoo colony of chimpanzees *Pan troglodytes*: development and management techniques. *Int Zoo Yearb* 26:236–48.
- Alford PL, Bloomsmith MA, Keeling ME, Beck TF. 1995. Wounding aggression during the formation and maintenance of captive, multimale chimpanzee groups. *Zoo Biol* 14:347–59.
- Baker KC. 1992. Hierarchy formation among captive female chimpanzees [Ph.D. Dissertation]. University of Michigan, Ann Arbor.
- Baker KC, Smuts BB. 1994. Social relationships of female chimpanzees diversity between captive social groups. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors. *Chimpanzee cultures*. Cambridge, MA: Harvard University Press. p 227–42.
- Baker KC, Seres M, Aureli F, de Waal FBM. 2000. Injury risks among chimpanzees in three housing conditions. *Am J Primatol* 51:161–75.
- Bloomsmith MA, Baker KC. 2001. Social management of captive chimpanzees. In: Brent L, editor. *The care and management of captive chimpanzees*. San Antonio, TX: American Society of Primatologists. p 205–42.
- Bloomsmith MA, Lambeth SP. 1996. Managing aggression in multi-male, multi-female chimpanzee groups. In: American Zoo and Aquarium Association (AZA) Regional Conference Proceedings. p 449–51.
- Brent L, Kessel AL, Barrera H. 1997. Evaluation of introduction procedures in captive chimpanzees. *Zoo Biol* 16:335–42.
- Cords M, Aureli F. 2000. Reconciliation and relationship qualities. In: Aureli F, de Waal FBM, editors. *Natural conflict resolution*. Berkeley: University of California Press. p 177–98.
- de Waal FBM. 1986. The brutal elimination of a rival among captive male chimpanzees. *Ethol Sociobiol* 7:237–51.

- de Waal FBM. 1992. A social life for chimpanzees in captivity. In: Erwin J, Landon JC, editors. Chimpanzee conservation and public health: environments for the future. Rockville, MD: Diagon/Bioqual. p 83–7.
- de Waal FBM. 1998 [orig. 1982]. Chimpanzee politics: power and sex among apes. Baltimore, MD: The Johns Hopkins University Press.
- de Waal FBM. 2000. Primates—a natural heritage of conflict resolution. *Science* 289:586–90.
- de Waal FBM, Hoekstra JA. 1980. Context and predictability of aggression in chimpanzees. *Anim Behav* 28:929–37.
- de Waal FBM, van Hooff JARAM. 1981. Side-directed communication and agonistic interactions in chimpanzees. *Behaviour* 77:164–98.
- Fritz P, Fritz J. 1979. Resocialization of chimpanzees. Ten years of experience at the Primate Foundation of Arizona. *J Med Primatol* 8:202–21.
- Fritz J, Howell S. 2001. Captive chimpanzee social group formation. In: Brent L, editor. The care and management of captive chimpanzees. San Antonio, TX: American Society of Primatologists. p 173–204.
- Fulk R, Garland C. 1992. The care and management of chimpanzees (*Pan troglodytes*) in captive environments. A husbandry manual developed for the Chimpanzee Species Survival Plan. North Carolina Zoological Society.
- Garner RL. 1896. Gorillas and chimpanzees. London: Osgood McIlvaine.
- Goodall J. 1986a. The Chimpanzees of Gombe: patterns and behavior. Cambridge, MA: Harvard University Press.
- Goodall J. 1986b. Social rejection, exclusion, and shunning among the Gombe chimpanzees. *Ethol Sociobiol* 7:227–36.
- Kollar EJ, Edgerton RB, Beckwith WC. 1968. An evaluation of the behavior of the ARL colony chimpanzees. *Arch Gen Psychiatry* 19:580–94.
- Kortlandt A. 1960. Can lessons from the wild improve the lot of captive chimpanzees? *Int Zoo Yearb* 2:76–80.
- Kortlandt A. 1966. Chimpanzee ecology and laboratory management. *Lab Primate Newsl* 5:1–11.
- McDonald S. 1994. The Detroit Zoo chimpanzees: exhibit design, group composition and the process of group formation. *Int Zoo Yearb* 33:235–47.
- Mottershead GS. 1959. Experiments with a chimpanzee colony at Chester Zoo. *Int Zoo Yearb* 1:18–20.
- Nieuwenhuijsen K, de Waal FBM. 1982. Effect of spatial crowding on social behavior in a chimpanzee colony. *Zoo Biol* 1:5–28.
- Nishida T, Hosaka K, Nakamura M, Hamai M. 1995. A within-group gang attack on a young adult male chimpanzee: ostracism of an ill-mannered member? *Primates* 36:207–11.
- Noë R, de Waal FBM, van Hooff JARAM. 1980. Types of dominance in a chimpanzee colony. *Folia Primatol* 34:90–110.
- Noon C. 1991. Resocialization of a group of ex-laboratory chimpanzees, *Pan troglodytes*. *J Med Primatol* 20:375–81.
- Pereira ME, Macedonia JM, Haring DA, Simons EL. 1989. Maintenance of primates in captivity for research: the need for naturalistic environments. In: Segal EF, editor. Housing, care and psychological wellbeing of captive and laboratory primates. Park Ridge, NJ: Noyes Publications. p 40–60.
- Pfeiffer AJ, Koebner AJ. 1978. The resocialization of single-caged chimpanzees and the establishment of an island colony. *J Med Primatol* 7:70–81.
- Pruetz JDE, McGrew WC. 2001. What does a chimpanzee need? Using behavior to guide the care and management of captive populations. In: Brent L, editor. The care and management of captive chimpanzees. San Antonio, TX: American Society of Primatologists. p 17–38.
- Reynolds V, Reynolds F. 1965. The natural environment and behaviour of chimpanzees *Pan troglodytes schweinfurthi* and suggestions for their care in zoos. *Int Zoo Yearb* 5:141–4.
- Riddle KE, Keeling ME, Alford PL, Beck TF. 1982. Chimpanzee holding, rehabilitation and breeding: facilities design and colony management. *Lab Anim Sci* 35:525–33.
- Sackett GP. 1991. The human model of psychological well-being in primates. In: Novak M, Petto AJ, editors. Through the looking glass: issues of psychological well-being in captive nonhuman primates. Washington, DC: American Psychological Association. p 35–42.
- van Hooff JARAM. 1973. The Arnhem Zoo chimpanzee consortium: an attempt to create an ecologically and socially acceptable habitat. *Int Zoo Yearb* 13:195–203.
- van Hooff JARAM. 1974. A structural analysis of the social behaviour of a semi-captive group of chimpanzees. In: von Cranach M, Vine I, editors. Social communication and movement. London: Academic Press. p 75–162.
- Wrangham RW, Peterson D. 1996. *Demonic males: apes and the evolution of human aggression*. New York: Houghton Mifflin.