# REHABILITATION OF CAPTIVE CHIMPANZEES

## (<u>PAN</u> <u>TROGLODYTES</u> <u>VERUS</u>).

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# ABSTRACT

The behaviour of 48 chimpanzees (*Pan troglodytes verus*) was studied over 27 months in Liberia, West Africa. The chimpanzees were first studied while they were housed in groups in enclosures in a medical research institute, and then after their release onto a 9.7 ha offshore island.

When the chimpanzees were observed in captivity, data on social behaviour were collected with the use of check sheets and *ad libitum* notes. Data were collected on aggression, social grooming, social play, sexual behaviour, and individual spacing. After release onto the island, data on both social and subsistence behaviour were collected with the use of *ad libitum* notes.

Both changes in social behaviour and in the development of subsistence behaviour were observed following release of the chimpanzees onto the island. Rates of aggression decreased following release, whereas rates of social grooming increased. Rates of social play decreased overall, but this was due to a decrease in social play by adults. Stereotyped or abnormal behaviour shown by some subjects declined. Subsistence behaviours which were observed following release were foraging for naturally occurring foods (leaves, fruits, seeds, and nuts), ant-eating, and tool-use for nut-cracking. Some subjects were also seen building sleeping-nests in trees . The chimpanzees also split into subgroups (including consortships) which showed similar trends in size and composition to those observed in wild populations of chimpanzees.

Some techniques found to be useful during the release process are discussed, and the study is compared to previous primate release projects.

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The author with Daniel (left) and Meryn (right).

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# CHAPTER 1

## REVIEW OF PRIMATE REHABILITATION PROJECTS

In order to put the present study in perspective, this chapter will outline some studies which have involved a change in environment for captive primates, ranging from resocialization of isolation reared individuals to release of captive primates to semi-free-ranging (with at least a 1 ha outdoor area, but some restrictions in travel-range) and free-ranging (with no restrictions in travel-range) sites.

Changes can be made to both the social and physical environment of captive primates. Extreme deprivation for a captive primate would be solitary housing in a small, barren cage, with little visual, auditory, olfactory, or tactile stimulation. In relation to the number of early studies which investigated the behavioural abnormalities produced by such environmental deprivation (e.g. NISSEN, 1951; BERKSON et al., 1963; BERKSON & MASON, 1964; HARLOW, 1964; DAVENPORT et al., 1966; SACKETT et al., 1976), few studies attempted to reverse the resulting behavioural abnormalities (SUOMI et al., 1972; CHAMOVE, 1978; ROSENBLUM & SMILEY, 1984).

For a highly sociable primate probably the most important change from solitary caging in a limited area is addition of a companion, and this would be expected to have a more beneficial effect on behaviour than, for example, doubling the cage size. Recent work with rhesus monkeys (REINHARDT et al., 1987, 1988) has shown that although introduction of a companion was not successful in all cases for previously isolated monkeys, 90 % of introductions of adult monkeys to infants were successful, and 83 % of introductions of adult female pairs were successful. Pairs were considered incompatible if the monkeys did not huddle, if one pair member constantly avoided the other, or was injured by the other. Compatible pairs huddled and groomed, and both had access to food. Three adult rhesus monkeys who had shown stereotyped behaviour when isolated gradually stopped this after introduction of a companion.

Improvements of environments for captive primates can perhaps be thought of as moving between points on a scale which ranges from an extremely deprived environment as described above to free-ranging in a natural setting. Captive primates whose environment is being improved can therefore be thought of as being moved from one point on this scale to another point, and the relative improvement can be judged from the beginning point and end point on the scale for the individual primate. Following transfer from one kind of environment to another, the primate concerned then goes through a period of adaptation to the new environment, during which time behavioural changes can be systematically recorded. Whether or not an individual primate can successfully adapt to the new environment will depend on the individual's history. Relevant factors are : the type of environment the primate was kept in, and, particularly for an extremely deprived environment, the length of time kept under these deprived conditions, and whether or not there are any resulting persistent behavioural consequences which limit the individual's adaptation to the new environment.

Captive chimpanzees have been kept in a wide range of environments, with one extreme being solitary caging in small, dark cages with no visual stimulation (e.g. NISSEN, 1951). At the other end of the range there are semi-free-ranging social groups of chimpanzees living in large outdoor enclosures, such as at Holloman Air Force Base, New Mexico (van HOOFF, 1967a; WILSON & WILSON, 1969). This colony had problems, however, which were taken into consideration in the design of the chimpanzee enclosure at the Arnhem Zoo in the Netherlands (e.g. van HOOFF, 1973a; de WAAL, 1982, 1984). In some cases captive chimpanzees have been released into natural environments and have become partly or totally self-sufficient (GRZIMEK 1970; BORNER, 1985; HLADIK, 1973; BREWER, 1978; CARTER, 1981, 1988). These examples will be discussed in turn.

## Resocialization of Captive Chimpanzees

FRITZ & FRITZ (1979; FRITZ, 1986) described the resocialization of 59 chimpanzees from a variety of backgrounds : laboratories, zoos, and circuses. They used the following 4 step index of socialization to determine the progress of each individual (FRITZ & FRITZ, 1979 : 203) :

1) Interaction of any kind, with chimpanzees or human beings.
2) Initiating tactile contact with another chimpanzee and demonstrating increased frequency in the number of contacts.
3) Initiating interaction with all members of a selected group of chimpanzees; the interactions may include aggression.
4) Ability to move from group to group or 'teacher' to 'teacher' with positive interaction; initiating and receiving all socially acceptable behaviours; ability to assume different roles in different groups.

The start of the resocialization process began in different ways, based on initial observations, life-history of the subject, and previous degree of contact with at least one other chimpanzee. There were 2 alternative grouping methods : one in which the new individual was immediately placed within a group, and another in which the new individual was put with one other chimpanzee and another 4 group members were gradually added. Individuals who were not thought to be ready for either grouping method were first caged next to a teacher, chosen for characteristics such as "gentleness" and "playfulness". The individual would then be caged together with the teacher and gradually the rest of the group would be introduced in pairs. All resocialized apes were wild-born. Only one adult male, kept in isolation for nine years, failed to achieve socialization. He carried out incessant stereotyped and self-mutilating behaviour and did not respond either to a teacher or to social units. All other individuals reached step 4 on the FRITZS' scale, the time taken to reach this stage being related to the individual's previous history. Individuals with previous olfactory, visual, auditory, and tactile (OVAT) communication with other chimpanzees took an average of 14.5 days to reach stage 4, those with OVA communication took an average of 138 days, and those with no previous contact took an average of 179 days to reach this stage. In general the FRITZS found that males were more severely affected by restricted rearing than females and that for males resocialization must begin at a younger age than for females (3-4 compared to 6-7 years) to be successful. Resocialization in terms of an individual being able to live in a group and exhibit appropriate social behaviour was 98% successful; in terms of eliminating all bad habits, the success rate dropped to 50%, and it dropped much further if the judgment hinged on whether or not individuals became breeders and parents.

The FRITZS' resocialization programme is the largest and most fully described one of its kind, but one other example of resocialization of chimpanzees is that of PFEIFFER & KOEBNER (1978; PFEIFFER, 1979; KOEBNER, 1981). PFEIFFER & KOEBNER worked with 8 chimpanzees, 2 of whom (*Larry* and *Janet*) were captive-born and had been kept for several years in an extremely deprived environment : small, dark, sheet metal cages which resulted in sensory, motor, and social deprivation. The other 6 were wild-born, kept in larger cages, and could see other chimpanzees. A resocialization procedure similar to the FRITZS' (1979) was followed, with pairs of chimpanzees being introduced in adjacent cages, then being caged together. Combinations of pairs were introduced and after four months the whole group was kept together. *Larry* and *Janet*, who originally could not climb and who showed a variety of stereotyped behaviour, gradually learned to climb (although they only did so when threatened), and they performed less stereotyped behaviour. *Janet* remained extremely withdrawn, and *Larry's* social behaviour was limited. If they were to be graded on the FRITZS' (1979) scale, *Janet* would probably have reached only the first point on the scale, and *Larry* the third point on the scale. After 5 months of living together, the 8 chimpanzees were then released onto a 0.13 ha island. This release shall be discussed further later.

Large Captive Groups of Chimpanzees

From the 1960's onwards, there has been a move towards improving captive environments for chimpanzees (MOTTERSHEAD, 1959a; REYNOLDS & REYNOLDS, 1965a; KORTLANDT, 1966; van HOOFF, 1967a), the goal being to establish colonies of mixed age and sex composition in spacious environments. One of the first large chimpanzee colonies was set up in 1966 by the Aeromedical Research Laboratory at the Holloman Air Force Base in New Mexico. Up to 43 chimpanzees were kept together in a 12 ha outdoor enclosure. The level of aggression within the group was found to be particularly high, however, particularly at feeding times (WILSON & WILSON, 1968, 1969). Other causes of aggression could have been eliminated if the enclosure had been more thoughtfully designed. For example, there was limited shade available in the hot, dry, barren enclosure, so individuals fought over access to shaded areas. There were also no objects provided for the chimpanzees to play with, and so fights arose over possession of the small number of objects found within the enclosure, such as sticks and rocks. From Table 1.1 it can be seen that the amount of space available per individual at Holloman was much higher than in other captive groups of chimpanzees which have been successfully housed together. The provision of a large amount of space is therefore not enough to guarantee the success of keeping chimpanzees together in large captive groups.

In the Netherlands,the Arnhem Zoo chimpanzee enclosure was designed in 1971 (van HOOFF, 1973a), with the aim of avoiding some of the mistakes which had been made in the Holloman colony. In mild weather (April - mid October), the chimpanzees have access to a 1 ha outdoor forested area (with most trees being electrically protected to prevent them being destroyed by the chimpanzees), which also contains climbing structures, car tyres, and pieces of rope. During the colder months of the year (mid October - March), the chimpanzees are kept in two large community halls with a total area of 650 square metres. These halls are equipped with climbing frames and "stamping platforms" (constructed of metal cylinders)to be used for play, as a visual barrier, or for aggressive displays. At first, 18 chimpanzees were introduced. One had been kept as a

**TABLE 1.1** Examples of Large Groups of Chimpanzees in Outdoor Enclosures.

| Location | Date set up | Outdoor area (ha) | Group size | sq.m. per indiv. | Age range (y) | Adult M; Adult F | Feeding routine | References |
|---|---|---|---|---|---|---|---|---|
| Holloman Res. Lab., New Mexico | 1966 | 12 | 35-43 | 2,791-3,429 | 1-18 | 6;18 | together | WILSON & WILSON (1968, 1969) |
| Arnhem Zoo, Netherlands | 1971 | a) 1<br>b) 0.6 | 23 | 435<br>261 | 1->25 | 4;9 | separate | van HOOFF (1973 a), ADANG et al. (1987) |
| Taronga Zoo, Australia | 1980 | 0.5 | 24 | 208 | 1->37 | 2;12 | separate | DAVIES (pers. comm.) |
| Edinburgh Zoo, Scotland | 1981 | 0.93 | 12 | 775 | 1-30 | 5;3 | together (a.m.)<br>separate (p.m.) | STEVENSON (pers. comm.), NASH (1982) |

a) enclosure area in summer
b) enclosure area in winter

pet; the others came from zoos and had been kept with up to 4 other chimpanzees. After one week 2 females had to be removed because they were being persecuted by the whole group, and after one month 2 females died (as a result of a bacterial infection), leaving a group of 14 chimpanzees. The adult females have successfully reproduced, however, bringing the group size to 23 in 1980 (de WAAL, 1984).

Many captive groups of chimpanzees contain only 1 adult male, perhaps because of fear of severe aggression between adult males, but at Arnhem 3 adult males were successfully kept together for 9 years. However, there was a fight between the 3 males in their indoor cage in 1980 which resulted in the death of 1 male (de WAAL, 1986). The study of the Arnhem chimpanzee colony has provided a rich insight into social interactions, relationships, and alliances among captive chimpanzees (de WAAL, 1978, 1982, 1984). FITCH et al. (1988) compared the behaviour of adult male chimpanzees in single-male and multi-male groups and found that levels of agonism were similar among all subjects.

Perhaps prompted by the example of the Arnhem Zoo chimpanzee colony, in the 1970's and '80's zoo enclosures for chimpanzees have been greatly improved (e.g. PAQUETTE & PRESCOTT, 1988), and chimpanzees are kept together in larger outdoor enclosures with structures for climbing, objects for play, and in some cases provision of structures which encourage natural behaviour, such as artificial termite mounds which encourage tool-use to obtain a food reward from inside (POULSON, 1974; BESCH, 1981; NASH, 1982).

There has also been a recent trend towards improving environments for chimpanzees in medical research institutes and brreding colonies (BLOOMSMITH et al., 1988; BLOOMSMITH, 1989; PRINCE et al., 1989; MOOR-JANKOWSKI & MAHONEY, 1989). This trend is hastened by the fact that those chimpanzees in the captive population who were wild-born are almost at the end of their reproductive years, and the majority of captive-born laboratory chimpanzees are proving to be inadequate mothers and breeders (SEAL & FLESNESS, 1986). In a move towards maintaining reproducing populations of chimpanzees, some laboratories have attempted to establish island breeding groups of chimpanzees.

In order to test the possibility that captive-reared chimpanzees might survive and reproduce in a semi-free-ranging setting in a North American climate, 8 chimpanzees from the Yerkes Regional Primate Research Centre were released onto a 9.6 ha coastal island in Georgia (SELLERS, 1973; WILSON & ELICKER, 1976). The first 4 chimpanzees released were a wild-born male and female (the female having been housed alone previously) and 2 captive-born females (1 restriction-reared). For 2 weeks before release, the chimpanzees were caged in different combinations of pairs, then all 4 were kept together a few days before release. The chimpanzees were released onto Bear Island in Georgia in June 1972, and all 4 survived for the following 6 months. They were provisioned (daily for the first 3 months, thereafter daily or every other day), but 3 also foraged for leaves, nuts, and fruits on the island. The captive-born, restriction-reared female was not seen foraging or climbing trees, and spent most of the time alone, frequently involved in stereotypic rocking, although she gradually became involved in more social interactions with others.

Two shelters were provided for the chimpanzees on the island, to allow some protection from wind, rain, and the colder winter temperatures (the seasonal mean temperature for the winter was 10.5 $^0$ C, compared to 26.5 $^0$ C for the summer). During the first winter on the island, the 2 restriction-reared females both died (1 from pneumonia, and the other resulting form a miscarriage and haemorrhage). The 2 remaining chimpanzees were showing signs of stress from the cold (shivering and reluctance to move) until straw was provided in the shelters , after which they used the shelters more and their condition improved.

In September 1973, 4 more chimpanzees (3 wild-born females, 1 with her juvenile daughter) were added to Bear Island. Although signs of stress from the cold were again seen in the winter, all 6 individuals survived the winter, and for at least the following 3 years.

Following the release of chimpanzees onto Bear Island, 8 chimpanzees from the Yerkes Regional Primate Research Centre were then released onto a 0.09 ha man-made island near Atlanta (DAVIDSON, 1975; ANON, 1975). This island was equipped with a heated shelter for winter months. Little data is available on this release, however.

<u>Rehabilitation of Primates</u>

The term rehabilitation is often used to cover a variety of procedures, some of which resemble or overlap with each other, but the following broad categories can sometimes be applied :

a)<u>Release</u> involves setting free captives, with or without following up their fate.

b)<u>Translocaton</u> involves capturing wild primates from one part of their natural range and moving them to another part, with minimum time spent in between in captivity.

c)<u>Reintroduction</u> is usually used to refer to placing primates into a suitable habitat that is currently lacking that species, as opposed to :

TABLE 1.2 Primate translocations and releases.

| Release site | Date | Species | No. Reld | wb/cb | Pre-release preparation | Provi-sioned | Nat. food | Follow-up | Outcome |
|---|---|---|---|---|---|---|---|---|---|
| Cayo Santiago isl., Puerto Rico | 1938 | Macaca mulatta | 400 | wb | N/A | + | + | + | reproducing popn. on island |
| Desecheo isl., Puerto Rico | 1966 | Macaca mulatta | 55 | from Cayo | N/A | (+) x | + | + | reproducing popn on island |
| Ohirayama Mountain, Japan | 1957 | Macaca fuscata | 81 | wb capt-10m | gp. formed before rel. | + | + | + | 8.5% died after release |
| Kao Tao, Thailand | 1965 | Macaca speciosa | 24 | wb capt-11m | none | x | + | (x) + | 45% not present 1 yr later |
| Enclosure, Texas | 1972 | Macaca fuscata | 156 | wb | N/A | + | + | + | reproducing population |
| Aligarh, India (moved 30km) | 1983 | Macaca mulatta | 20 | wb | N/A | (+) x | + | + | reproducing population |
| Cayo Santiago isl., Puerto Rico | 1939 | Hylobates spp. | 14 | wb capt-1y | none | + | ? | + | attacked humans, removed after 2 yrs |
| Ko Klet Kaeo isl., Gulf of Thailand | 1966 | Hylobates spp. | 20 | wb from lab | none | + | + | + | 60% died, disapp. or removed. Ended in 1970 |
| Hall's island, Bermuda | 1970 | Hylobates spp. | 10 | wb from lab | none | + | ? | + | 50% died. Project assumed discontinued |
| Saiyok, Thailand | 1976 | Hylobates lar | 31 | wb & cb | none | (+) x | ? | (+) | 6.5% died, only 12.8% seen > 1m after release |
| Santa Sofia isl., Colombia | 1967 | Saimiri sciureus | 5690 | wb | N/A | (+) x | + | (x) + | 83% died (from 1972 population estimate) |
| Zebra isl., Lake Kariba, Rhodesia | 1977 | Cercopith. pygerythrus | 17 | wb pets | fed nat. foods shown predators | x | + | (x) + | reproducing population on island |
| Laikipau Plateau, Kenya (moved 90km) | 1984 | Papio anubis | 131 | wb | N/A | (+) x | + | + | 4.6% disappeared |
| Poço das Antas Reserve, Brasil | 1984 | Leontopith. rosalia | 14 | 13 cb 1 wb | practice in foraging and locomotion | (+) x | + | + | 85% died, killed, or returned to captivity |

wb/cb - wild born/captive born
N/A - not applicable
Provisioned, (+) x - provisioned on release, then discontinued
Nat. food, + - eat at least some natural foods

? - unknown
Follow-up, (x) + - not monitored at time of release, but at least one follow-up study later
Follow-up, (+) - follow-up study for only a short time after release

d)Introduction, which refers to putting a primate species into a habitat where it has never naturally occurred.

e)Rehabilitation in its strictest sense involves training inadequate individuals in skills which allow them to survive with greater independence.

The primate releases (Table 1.2) which follow fit mainly into the category of translocation, and the great ape releases (Tables 1.3 and 1.4) fit mainly into the category of rehabilitation, but there are some exceptions, and some projects which overlap categories, therefore the general term of release shall be used to cover all projects in the following section. The aims underlying projects discussed vary from establishing breeding colonies of a species to supply individuals for medical research (e.g. TSALICKIS, 1972), to moving a species from an unsuitable wild habitat to a more suitable one (e.g. STRUM & SOUTHWICK, 1986), to restoring an endangered species to its natural habitat to aid the conservation of a species (e.g. KLEIMAN et al., 1986). Despite these different aims, however, all projects involve moving groups of primates from one habitat to another, and although the group's adaptation to the new environment was not specifically studied in most cases, some information may be gleaned from the outcome of the projects. For instance, the survival rate, if given, can be used as a crude measure of how successful the released group was in adapting to the new environment, and if there was no provisioning it can be concluded that the group learned to find natural food in the new environment.

The primate release project table (Table 1.2) is split into macaque releases, then gibbon releases (since there are several examples for these species), then other species follow. Within each section projects are listed in chronological order, which is also the order they shall be discussed in.

## Macaque Releases

One of the earliest primate releases was carried out in 1938, when 400 wild-born rhesus macaques (*Macaca mulatta*) from India were released onto Cayo Santiago, a 15 ha island in Puerto Rico (CARPENTER, 1942; ALTMANN, 1962; CARPENTER, 1972). The macaques were able to find some food on the island, but were also regularly provisioned. During the period of provisioning, the population increased and large numbers of macaques were removed and sold for medical research, but provisioning then became irregular and there was a decrease in population and signs of starvation until regular provisioning was resumed in 1950. In 1966, one group of macaques was transferred to Desecheo Island, a 122 ha island in Puerto Rico (MORRISON & MENZEL, 1972). Provisioning was not required on this larger island, and the group became self-sufficient.

A project involving Japanese macaques (*Macaca fuscata*) began in 1956, with the aim of establishing a free-ranging, but provisioned colony of monkeys for behavioural research (KAWAI, 1960). First, 81 macaques were captured from different wild groups, then introduced in an outdoor enclosure over a period of 10 months to form one group, which was then released on Ohirayama Mountain, Japan. The site of the outdoor enclosure was also the site for provisioning when the macaques were released. KAWAI found that on release the macaques were very reluctant to eat wild foods other than two plant species which were familiar from the area they were captured from. However, it should be noted that the release area was chosen for its paucity of suitable wild foods because the aim was to make the macaques dependent on human provisioning so that they would remain in the area and could be studied. The macaques were at first reluctant to come to the provisioning site and at least 5, possibly 7 individuals died. A small group of 6 separated from the main group and were believed to have survived, but the majority of the released group soon became used to human provisioning at the feeding site and stayed in the area.

Another project which involved releasing wild-born macaques who had spent some time in captivity into a free-ranging site was carried out in Kao Tao, Thailand, in 1965 (BERTRAND, 1969). These were 20 stumptail macaques (*Macaca arctoides*) who had been in captivity for 11 months. One year after release 11 individuals were still in the release area and another four individuals who were caught 200 km away were successfully added to the group by BERTRAND. On surveying the area, BERTRAND found no groups of stumptail macaques which were not being disrupted by trapping or shooting, except in protected areas or in dense forests. The Kao Tao group lived under the protection of a Buddhist Temple and in spite of proximity to the village was completely wild. BERTRAND chose this group as the only one convenient for a short study, and her study remains the only field study of stumptail macaques. If this group had not been transferred 700 km from its original habitat to a protected area when extensive trapping of the species was going on, there may have been no data available on this species of macaque free-ranging in its natural environment.

In the late 1960's, a troop of Japanese macaques (*Macaca fuscata*)living near Kyoto split into two groups after an increase in numbers. Following the split one troop displaced the other, which was forced to leave its original range and moved to nearby gardens and temples. To prevent this troop of 156 macaques being destroyed, it was donated to the University of Wisconsin, transported to the United States in 1972, and released in a 100 acre fenced enclosure in Loredo, Texas (BRAMBLETT et al., 1981). In the late 1970's this troop had increased in numbers to 279. Although no data are given on provisioning, presumably the troop was at least partially provisioned, perhaps less so in the fruiting season when abundant fruit was available. In 1980 the troop was moved to a 50 acre enclosure in Dilley, Texas. The enclosure was surrounded by an electric fence, but some individuals climbed it and escaped. Some returned and some died (BRAMBLETT et al., 1987) but numbers are not given.

A more recent translocation project for a species of macaque was carried out in 1983 when a sub-group of 20 rhesus macaques (from a group of 130) was transferred 30 km from the group's original location in Aligarh District in India (SOUTHWICK et al., 1984; STRUM & SOUTHWICK, 1986). The aim was to relocate this sub-group from a high-density population to a suitable habitat which formerly contained the species. The project was viewed as a pilot study on the restoration of rhesus monkeys to suitable habitats. The new habitat had more natural foods, better cover, and was further from human habituation than the groups original location. The group was unsettled in the new habitat for several weeks despite daily provisioning. Three juveniles disappeared, but returned several months later. The group was provisioned for five months, but by the third month had moved 2 km from the release site to settle next to a village. The group then subsisted on a combination of natural foods and handouts from the villagers, which was similar to the situation in their original location. This became the group's fixed range and it was adopted by the villagers. Eight months after release, 3 other rhesus joined the translocated group, so the groups transfer may have provided additional opportunities for inter-group transfer for rhesus in this area.

Gibbon Releases

Four projects involving releasing gibbons from captivity are listed in Table 1.2. Three of these were releases onto islands and one was a release into natural forest area inhabited by wild gibbons. The first release of 14 gibbons was in 1939 onto Cayo Santiago Island, Puerto Rico (CARPENTER, 1972). This was a 15 ha island already inhabited by 400 released rhesus macaques (described above). Six of these gibbons had been in captivity for one year and the other 8 for only a short period after capture and shipment. Three (3.7 x 3.7 x 2.4 m) cages were built on the island for controlled release and for feeding (to eliminate competition for food by macaques). When released, however, the gibbons repeatedly attacked observers and caretakers and so after their first year on the island they were kept in the cages most of the time and only selectively released. The expense of maintaining the gibbons in cages rather than free-ranging, their aggressiveness towards people, and the killing of the first and only gibbon infant born on the island by macaques led to the decision to remove them from the island two years later in 1941.

In 1966-67 the Seato Medical Research laboratory released 20 gibbons onto Ko Klet Kaeo Island, a 25 ha forested island in the Gulf of Thailand (BERKSON et al., 1971; BROCKELMAN et al., 1973, 1974). Their aim was to explore new methods of breeding gibbons for use in medical research. Although 20 gibbons were released, there were never more than 14 individuals on the island at one time. By 1970, 12 gibbons (6 of each sex) had either died, disappeared or had been returned to the laboratory either because they had not remained paired or because they had been too aggressive towards humans or other gibbons. The gibbons were provisioned, but some relied mostly on natural foods. BROCKELMAN et al. (1973, 1974) studied their social interactions and found that during their first 2 years on the island some groups contained 3 or 4 individuals, but gradually monogamous pair bonds formed and pairs established territories. The first births on the island did not occur until these pair bonds had become established, then 4 infants were born. There were also 30 crab-eating macaques (*Macaca fascicularis*) on the island, but they interacted very little with the gibbons. The project ended 4 years later in 1970, and the gibbons were returned to the laboratory. Two of those returned to the laboratory were released 6 years later into a natural forest in Saiyok, Thailand (see below) when the colony was no longer required for medical research.

A free-ranging colony of gibbons was established on Hall's Island in Bermuda in 1970, to be used for a study on experimental modification of behaviour in an open-field situation. Brain implants were used to stimulate and inhibit aggression in gibbons in the laboratory and on Halls Island. Of 10 gibbons released from 1970-71, 5 had died by 1972 and one had been removed because he was behaviourally aberrant (BALDWIN & TELEKI, 1976).

The final gibbon project (TINGPALAPONG et al., 1981) involved releasing 30 gibbons from a medical research laboratory into a 225 sq km area of dense forest in Thailand. Beginning in 1976, over a period of 17 months, 26 adults and 4 infants were released. The adults had spent an average of 10.3 years in captivity and were mostly male-female pairs, some with infants which were released with them. Two methods were used for releasing the gibbons. The first method involved constructing 2 cages (3 x 3 x 3

m) in the forest, from which the gibbons were released and to which they could return for provisioning. Of 15 released in this way, 10 were seen periodically entering the cages for food in the first week then were not seen again. The other 15 gibbons were released straight into the forest with no base where they could come for provisioning. Most of these 15 were not seen again after release. Some of the gibbons were tame and seeked human company. Three of these were re-released deeper in the forest after they had accompanied humans or turned up at local residences. One female was released a further 2 times, but each time sought out humans, and since she was also losing weight she was not released again. Of the 17 adults observed after release, 7 were seen eating natural foods. Only 4 individuals were seen more than one month after their release. These 4 are stated to have been "accepted into groups of wild gibbons" (TINGPALAPONG et al., 1981), which seems unlikely considering some aggressive encounters with wild gibbons were seen, and 2 adult males had cuts on their feet resulting from fights with wild gibbons in the area. The large number of disappearances following release and the lack of follow-up prevents the calculation of the success rate of this project, and it can only be said that 4 of the 31 individuals survived for more than one month.

Other Species

Other than these projects releasing macaques and gibbons, 4 projects have involved other species : squirrel monkeys (*Saimiri scuirus*), vervet monkeys (*Cercopithecus pygerythrus*), baboons (*Papio anubis*) and golden lion tamarins (*Leontopithecus r. rosalia*).

From 1967-1970, 5690 (as reported by TSALICKIS, 1972, but later disputed by others: see below) wild-caught squirrel monkeys were released onto Santa Sofia Island, a 44 ha island in Colombia. The aim was to maintain a breeding population of squirrel monkeys for export to the United States. Large numbers of pregnant females captured on the mainland were released onto the island rather than being exported because they often aborted and/or died during transport to the United States. Adult males were also released onto the island to maintain a sex ratio of approximately 1 male to 4 females. The monkeys were occasionally provisioned and large areas of fruits and crops (10 ha bananas, 4 ha papaya, 4 ha guava, 2 ha corn) were planted as a source of food for the monkeys. However, more than 90% of the island was covered by water in the rainy seasons, which destroyed most of the crops (SPONSEL et al., 1974).

TSALICKIS (1972) estimated a birth rate of 80% during the first year, and assumed this birth rate was maintained in subsequent years. On the basis of the number of monkeys released on the island and assuming no mortality, he estimated that the population on the island was 20,689 in 1971. However, when a census was carried out in 1972 (SPONSEL et al., 1974; BAILEY et al., 1974) the population was estimated to be 850-966, which showed that previous population increase estimates were not only unreliable, but also there was a substantial decrease in population if 5690 monkeys were originally released. JERKINS (1974) stated that the greatest problem in the diminishing population was poaching of the squirrel monkeys on the island to sell them for export. In 1973, a tattooed monkey from the original release group was found in a shipment for a zoo in Florida. Also in 1972, some monkey traps were reported to have been found on the island. However, although some poaching may have occurred, it seems unlikely that it was the major cause for the diminishing population. A more likely cause would be mortality from a combination of factors such as disease, starvation, and stress.

In 1977, WILSON (1980,) released a group of 17 vervet monkeys onto an island in Lake Kariba, Rhodesia. They were all wild-born and most had been kept as pets until they were adults. WILSON prepared them for release by keeping them together until they had formed a stable group, feeding them wild foods, showing them potential predators, and minimising human contact so that in time they avoided humans. They were then released onto Zebra Island in Lake Kariba. Provisioning was felt to be unnecessary, but unfortunately there was little follow-up of the released monkeys. In 1979, however, 19 monkeys, 3 with infants, were observed on the island indicating that most of the group must have survived.

In 1984, 3 troops of baboons from Gilgil, Kenya, a total of 131 individuals, were trapped and translocated to a site 190 km away (STRUM & SOUTHWICK, 1986). The reason for the move was that agriculture in their original home range was increasing and they were becoming pests, also it was hoped that the project could help to evaluate the feasibility of translocation as a management and conservation tool. STRUM states that the most difficult part of the translocation was finding a suitable release site taking into account ecological factors, the distance from agricultural areas, and the general accessibility. Before trapping, the baboons were habituated to open baited traps until they all readily entered them. Each troop was then trapped in its entirety with the exception of 1 male who escaped and could not be recaptured. The baboons were then transported to the release site. Two methods were used to help prevent each troop from immediately leaving the release site : the subadult and adult males were held captive for several days to give a focal point for the rest of the troop, and the troop was provisioned at this site for several weeks. These methods were found to work in maintaining the troops as cohesive social units. From the first day of release, the baboons ate both familiar and unfamiliar natural foods, and from the third week provisioning was continued only to orient the baboons rather than being a necessity. Two troops suffered no mortality following the translocation, but 6 immatures disappeared from the third troop. They were assumed to have died from starvation during a drought period when they were not provisioned. The troops were then provisioned until the end of the drought period and no further mortality occurred. Aggression from local baboon troops was short-lived and within several weeks a male had transferred in from the indigenous population. Nine months after their release, 2 of the troops appeared to have a large and relatively stable home range. At this time translocated males also began to transfer into indigenous troops. In less than a year the translocated baboons had therefore adapted to their new environment and become integrated into the indigenous baboon population.

The final project in Table 1.2 is a release of golden lion tamarins (*Leontopithecus r. rosalia*). In 1984, 14 golden lion tamarins were released into the Poço das Antas Reserve in Brazil (KLEIMAN et al., 1986). Thirteen of these tamarins were captive-born in the United States, then transferred to Brazil for a 6 month period of quarantine and preparation prior to release. This appears to be the first release of captive-born monkeys. During the period of preparation , 1 wild-born individual was added to the release group.

Pre-release preparation for the tamarins included practice in foraging for hidden and embedded food. Adults were found to be much less likely to open embedded food-sites. The frequency of opening embedded sites for each individual before release was found to be correlated with number of days of survival (before death or rescue) after release. Monkeys that were more adept at opening embedded sites survived longer.

The tamarins were also provided with whole fruits and many natural foods, including insects, frogs, and lizards. The tamarins readily accepted live prey, but did not discriminate between dangerous and non-dangerous species. When a toad (*Bufo marinus*) was presented, 2 tamarins bit it before it was removed. These 2 became extremely ill and frothed and vomited, then went into convulsions, while the others watched. They still tried to get to the toad the following day, however, when it was presented in a glass jar. Neither the affected nor the observing monkeys seemed to have learned from the near-fatal encounter.

During preparation, the tamarins were also encouraged to jump, climb and hang, to develop motor skills. Following release, however, they were still reluctant to use natural vegetation of various textures, diameter, and flexibility, and they were unable to plot a cognitive route through the forest between themselves and an incentive. They often descended from trees and travelled on the ground, which resulted in 1 tamarin being killed by a feral hunting-dog.

Before release into the forest, the tamarins were kept in their release groups in cages in the forest for 12 - 29 days to allow them to acclimatise to the environment. The tamarins were provisioned for 9 - 11 months following release, but 1 year after release only 3 of the 14 released were still known to survive. The other 11 had died or been removed. Causes of death or debilitation included: disease (5), disappearance (2), predation (1), exposure (1), snake-bite (1), and social conflict (1). Most losses occurred shortly after release, and the major cause of mortality was a disease that resulted in the death of 5 tamarins (7 months after release).

The tamarin release was therefore not very successful, despite pre-release preparation. Adults showed poorer performance than younger tamarins during foraging training and also had apparently greater deficits in motor ability. When age and the number of days of survival were compared, a statistically significant difference was found. KLEIMAN et al. (1986 : 976) concluded that young tamarins were "more likely to have the vitality and behavioural flexibility to survive the dramatic environmental changes between life in a zoo cage and life in the Brazilian forest."

## Great Ape Release Projects

Rehabilitation has been attempted with 3 of the 4 species of great apes: mountain gorilla (*Gorilla gorilla beringei*), orang-utan (*Pongo pygmaeus*), and chimpanzee (*Pan troglodytes*).

An infant mountain gorilla confiscated from poachers was cared for by FOSSEY (1981,1983) for 3 months and after 1 unsuccessful attempt, was then successfully introduced into a second wild group. One year later, however, the infant died of pneumonia after a long period of heavy rains. This seems to have been the only attempt at restoring gorillas to the wild.

Five orang-utan rehabilitation projects are listed in Table 1.3. The orang-utans in all projects were wild born and were either confiscated from hunters when very young, or had been kept as pets for a number of years. Details on specific rehabilitation procedures used are not available for all projects, but they all involved a similar general procedure of setting up a feeding station in the forest, taking young orang-utans for walks in the forest, and encouraging them to climb in trees and to become more independent. Sometimes individuals who were felt to be capable of surviving on their own but who did not leave the rehabilitation centre by choice were transferred to another area of forest.

The first orang-utan rehabilitation project began in Sarawak in 1961

TABLE 1.3 Projects which have sought to rehabilitate Orang-utans.

| Release Site | Date Reld. | No. Reld. | Ages (y) | Background (see below) | Pre-rel. prep. | Provisioned | Follow-up | Outcome |
|---|---|---|---|---|---|---|---|---|
| Sarawak, N. Borneo | 1961 | 3 | 1-3 | w-b | + | + | + | 1 died, 2 moved to Sepilok (below) |
| Sepilok, N. Borneo | 1964-88 | ~ 200 | 1-12 | w-b | + | (+) x | + | "only a small proportion fully adapt" |
| Ketambe, N. Sumatra | 1971-74 ? | > 31 | <1-9 | w-b | + | (+) x | + | ? died, 8 killed } 100 rehabilitated in 4 years between 2 projects |
| Bohorok, N. Sumatra | 1971-74 ? | > 50 | 1-10 | w-b | + | (+) x | + | } 100 rehabilitated in 4 years between 2 projects |
| Kalimantan, S. Borneo | 1972-88 | > 14 | 1-7 | w-b | + | (+) x | + | ? (some rehabilitated) |

Subjects from all projects come from one of two backgrounds : they were either cofiscated from hunters when very young, or were kept as pets for a number of years, then donated to the projects.

See TABLE 1.1, page 8 for key.

(HARRISSON,1963) with 3 infants, but ended for political reasons in 1964. Two survivors were transferred to a newly established rehabilitation station in the Sepilok Forest Reserve in Sabah (de SILVA,1971). From 1964 to 1969, 41 orang-utans were involved in this project: 10 died, 7 left the area, and 24 remained either at the station or visiting it occasionally from the forest. A more recent report by PAYNE (1987) states that nearly 200 orang-utans have been released into the forest in this project, of which "only a small proportion" have fully adapted to life in the forest.

Two further projects were set up in northern Sumatra by BORNER (1979) and by RIJKSEN & RIJKSEN-GRAATSMA (1975; RIJKSEN,1978). Of 31 individuals involved in the latter project between 1971 and 1974 , 8 were killed by a clouded leopard, 4 died, 6 disappeared, and 4 were transferred to another area of forest. Only 2 individuals left the rehabilitation centre of their own accord and were known to have successfully integrated into the wild population. The other 7 remained near the centre. BORNER (1979) stated that in 4 years at least 100 orang-utans were successfully rehabilitated between the 2 projects, whereas RIJKSEN (1978) stated that in 5 years fewer than 100 individuals were rehabilitated. Perhaps RIJKSEN's criteria for successful rehabilitation are stricter, since he includes positive social contact with wild orang-utans as well as regularly staying away from provisioning. It should be noted also that sometimes the term "rehabilitated" was used for orang-utans who had left the rehabilitation centre, even when there were no follow-up data to determine whether they had died or were living free.

A fifth project is that of GALDIKAS (1975,1980) who has worked with at least 14 infant orang-utans in the Tanjung Putung Reserve in Kalimantan (Borneo). There seems to be little published data on the failure or success of this project, although GALDIKAS does say briefly that animals that had been kept as pets for several years could take a little longer to become used to the forest. However, even a female that had been kept for 6 years in a small cage and who could not walk when she arrived at the rehabilitation centre, was successfully rehabilitated, consorted with a wild male, and gave birth. Hence, although past experience could lead to different lengths of stay at rehabilitation centres, at least some orang-utans from almost every background have been successfully rehabilitated.

Six projects for rehabilitating chimpanzees (*Pan troglodytes*) are listed in Table 1.4. These projects vary widely in factors such as the background of the individuals in the project and the amount of preparation and follow-up carried out, but all have shown some successes and some failures. The release sites vary from an island of 0.13 ha to

TABLE 1.4 Projects which have sought to rehabilitate Chimpanzees.

| Release Site | Date Released | No. Reld. | Ages (y) | Background | Pre-rel. Prep. | Provis-ioned | Follow-up | Adaptive Behaviour | Outcome |
|---|---|---|---|---|---|---|---|---|---|
| Rubondo isl., Tanzania, 2400 ha | 1966-69 | 17 | 4-12 | w-b from zoos | x | x | x | 1,2,? | repd. popn. on island |
| Ipassa isl., Gabon, 65 ha | 1968-72 | 8 | 4-8 | w-b from lab | x ? | + | + | 1,2,4,6 | 2 escaped others removed |
| N.K. Nat. Park, Senegal | 1973-75 | 8 | 1-6 | 6w-b 2c-b | ++ | + | + | 1,2,4,5,6 | moved to island in River Gambia |
| Baboon isl., Gambia, 490 ha | 1979 | 9 | 1-13 | 7w-b 2c-b | ++ | + | + | 1,2,4,6 | added to above group |
| 0.13 ha isl., Florida | 1975 | 8 | 4-11 | 6w-b, 2c-b from lab | + | + | + | 2 (crude) | ? |
| 3 islands, Liberia, 6, 27 & 28 ha | 1978<br>1983<br>1985 | 18<br>24<br>22 | 5-20+ | w-b from lab, some pets | + | + | + | 1,2,3,5 | repd. popns. on islands |

Adaptive Behaviour :
1) eating wild foods
2) nest-building
3) ant-eating (without tool-use)
4) ant-dipping/termite fishing
5) stone tool-use (for nut-cracking)
6) predatory behaviour

See TABLE 1.1, page 8 for key.

free-ranging in a National Park, but the background of the individuals concerned should be considered in relation to the release site, since all involve a vast change in environment for the subjects involved.

The first of these projects began in 1966, when 17 chimpanzees were released onto Rubondo, a forested island of 2400 ha in Lake Victoria, Tanzania (GRZIMEK,1970; BORNER,1985). All individuals were wild-born, but had spent between 3 1/2 months and 9 years in captivity under conditions which varied from solitary confinement in small cages, to better caging in groups. They were mostly chimpanzees from European zoos which were not wanted because they were so aggressive towards people, so not surprisingly the main problem with this group following release was that they attacked people. They were released in 4 groups from 1966 to 1969, but there was no close monitoring in the months following their release so it is not known which individuals survived. Of the original 17 at least 2 females were still alive in 1985, and there was then a free-ranging population of at least 20 chimpanzees on the island (BORNER,1985), including some second and possibly third generation chimpanzees born on the island. Those chimpanzees who were born on the island avoid people, so aggression towards people is no longer a hazard.

The next rehabilitation project involved releasing 8 chimpanzees from a medical research laboratory onto a 65 ha island (Ipassa) in Gabon, in 1968 (HLADIK,1973,1974). All were wild-born and had been in captivity from a few months to several years. Although they were given supplemental food, particularly when there was low fruit production, the apes found many natural foods on the island. Besides fruit, they ate leaves and stalks, ants, small mammals, birds, and birds' eggs. The chimpanzees built nests in trees each evening to sleep in. This group of chimpanzees remained on the island until 1978 when they discovered that they could wade across the river to its banks at low tide. Most of the group were captured and taken to a medical research laboratory but at least 2 or 3 individuals escaped. One female who escaped was later observed with an infant (GAUTIER-HION, pers. comm.).

A rehabilitation project with a different approach was that of BREWER (1978,1982). This was also the first project to attempt to release chimpanzees into a free-ranging site. BREWER worked intensively with her group of mostly young chimpanzees, teaching them skills needed for survival by serving as their role model. She taught them which foods to eat and when necessary, the techniques needed to get these foods, such as using stones to crack open hard-shelled fruits or pods and using twigs for termite fishing. She also taught them how to build nests in trees and actively discouraged them from sleeping on the ground. Their training began in the Abuko Nature

Reserve in The Gambia, and continued at Mt. Asserik in the Niokolo-Koba National Park in Senegal. At Mt. Asserik, the chimpanzees became increasingly self-sufficient, but they also began to encounter wild chimpanzees in the area who reacted hostilely to the newcomers. When the wild chimpanzees started coming to the camp area and attacking the rehabilitants there, BREWER decided to remove them for their own safety. In 1979, they were taken to Baboon Island National Park in the River Gambia, The Gambia, where they remain today.

CARTER's (1981, 1988) project is linked to that of BREWER. Working with a group of 9 chimpanzees from mixed backgrounds (some captive-born, some wild-born), CARTER began with an 18-month training period at Abuko Nature Reserve. There, the captive-born chimpanzees in particular had to be taught to accept wild foods. They were then moved to a 490 ha island in the Gambia River where CARTER lived with them, teaching them many of the things that BREWER had taught her chimpanzees. An added problem with one chimpanzee was not only had she been born in captivity, but she had been raised in a human family with no contact with other chimpanzees (TEMERLIN,1975), so she had to learn appropriate social behaviour . Thus, she needed more intensive training than did other group members but progressed well. Most of the apes from BREWER and CARTER's groups have now been introduced so that one large community has been formed, and several females are rearing wild-born offspring.

All of the rehabilitation projects mentioned above have produced at least some individuals who were able to survive in a natural environment without provisioning, but not all chimpanzees can successfully learn the skills needed for surviving in the wild. For example, one project involved taking on a set of apes who had suffered the most extreme forms of environmental and social deprivation (PFEIFFER & KOEBNER ,1978; KOEBNER,1981). The aim was not to produce chimpanzees capable of surviving in a natural environment, but to resocialize individuals kept in isolation for long periods and to establish an island breeding colony for behavioural research. The results are instructive in showing that the varying degrees of success of the other projects was probably much related to the past experiences of the individuals involved.

The resocialization of PFEIFFER & KOEBNER's group of 8 chimpanzees was described above. After 4 months of living together in various combinations, the 8 chimpanzees were kept together for 5 months before being transferred to a 0.13 ha island in a safari park in Florida. The female from the very deprived environment remained in an enclosure on the island for 4 weeks until she was coaxed out with food and the door was blocked behind her. Six weeks later she was found dead; apparently she failed to avoid being bitten by a hippopotamus which lived in the moat surrounding the island. Another

2 individuals who had showed stereotyped rocking in captivity showed a reduction in this behaviour following release and the male from the very deprived environment showed some improvement in locomotion and in social behaviour, but his social life always remained limited. The island that this group was released onto was small and bare, which rules out the possibility of comparison with the adaptive behaviour observed in other projects, but from the data available it seems unlikely that these apes could have adapted as well as apes in other projects. However, even release onto a small island was a vast change in environment and had clear effects in normalising the chimpanzees' behaviour.

The last project on Table 1.4 is the present study project, which shall be described in the following chapters. Many of the primate release projects discussed in this chapter reported little or no data on the success of the project, or on the adaptation of the primates released into a new environment. The aim of the present study was to systematically record the behaviour of a group of chimpanzees while in captivity, then following their release onto a natural island. The comparison of individuals subjects' behaviour was planned to determine the factors which might influence the likelihood of successful adaptation to a new environment. I also hoped that comparison of data collected in this study with those from other release projects would give useful information which might lead to improvements in future release projects.

# CHAPTER 2

## METHODS

### STUDY AREA.

i) Laboratory - Subjects were housed at a medical research laboratory in Liberia, West Africa (Figure 2.1). They were housed in open-air enclosures (Figures 2.2 and 2.3) surrounded by a 5 m high concrete wall with barred window sections allowing visual access to the surrounding environment (with a partial view of other laboratory buildings, but mainly views of grassland and secondary forest areas). The area of these enclosures was 160 $m^2$ and the base was covered in sand. A shelter with concrete base, walls and roof measuring 2x1x1.2 m was situated in the middle of each enclosure and on top of this was a climbing frame with a car tyre suspended from each end by 1m of chain. There were also 2 or 3 loose tyres in each enclosure. At the rear of each enclosure there were 2 adjoining cages measuring 2x1.3x2.5 m, which had doors operated by a pulley system and which were used to separate individuals from the group or to add new individuals to the group. Through these cages and across a central area in the middle of the building, animals could look at the groups of chimpanzees in other enclosures.

Chimpanzees slept inside the shelters, on tyres, or on the sand floor of the enclosures. Food (assorted fruits and bread) was dropped into the enclosures from above and milk was given out in cups at the windows of the enclosures. When enclosures needed cleaned, the chimpanzees were locked into holding cages to allow staff to enter and clean the enclosures.

Prior to being housed in these enclosures, individuals had been kept in cages of varying sizes, the smallest measuring 2.5x2.5x2 m The smallest were constructed of wire mesh and the largest of iron bars. All cages contained 2 or more wooden shelves at various heights and a car tyre suspended on a chain.

ii) Island - The subjects were released onto a 9.7 ha island (Island A) surrounded by mangrove swamp which allowed access to another island (Island B) 17.4 ha in area (Figure 2.4). The total dry land area available to the animals was therefore 27.1 ha and the mangrove swamp area was 85 ha. Both islands were separated from a third island (Island C, 26 ha) containing another group of chimpanzees by a man-made canal 900 m long, 6 m wide and 1.5 m deep (see Figure 2.4). The canal was made before the study group was released to prevent chimpanzees from different island groups travelling

**FIGURE 2.1** Distribution of *Pan troglodytes* in Africa, and location of study area.

Adapted from GOODALL (1986), based on TELEKI's data.

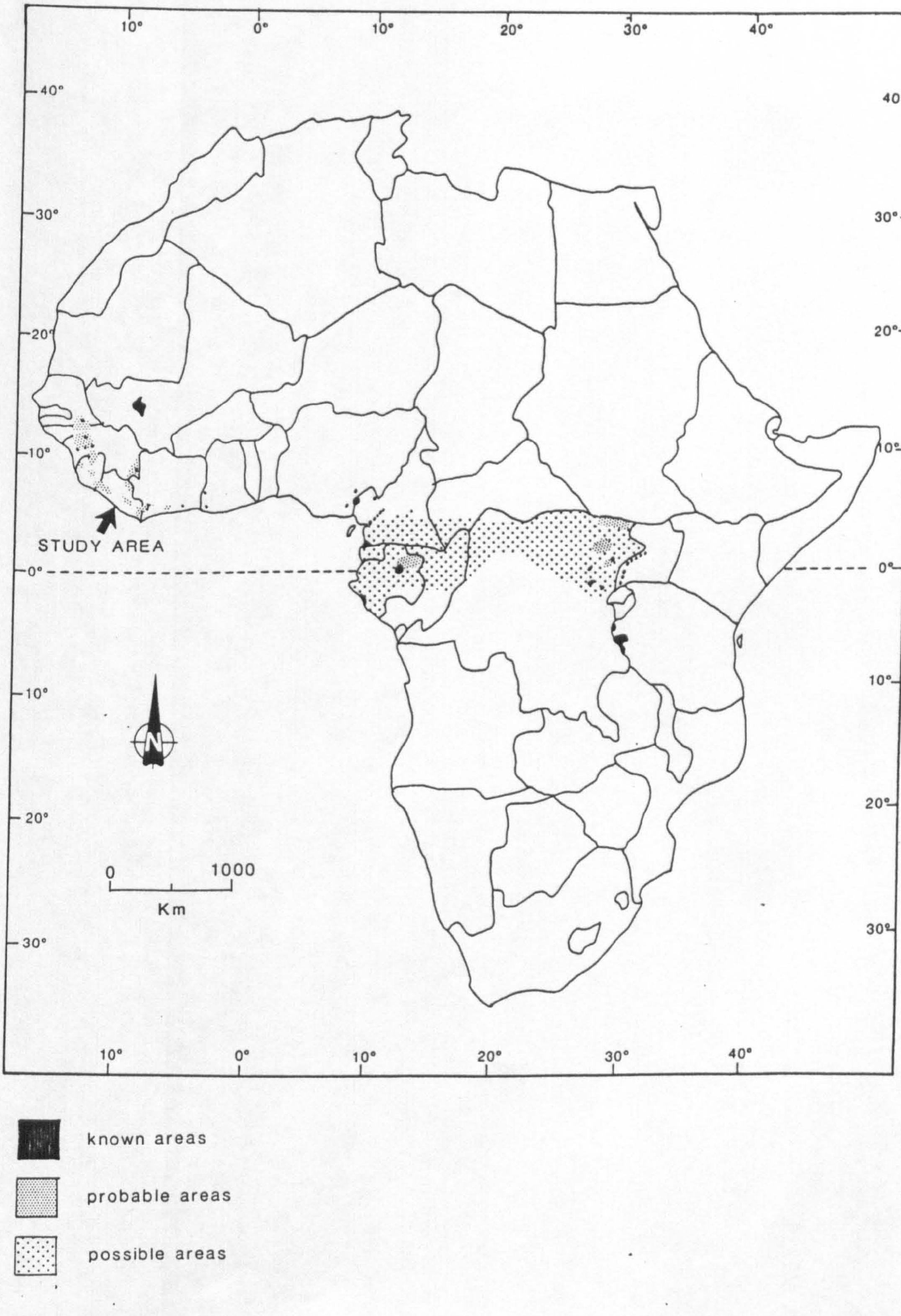
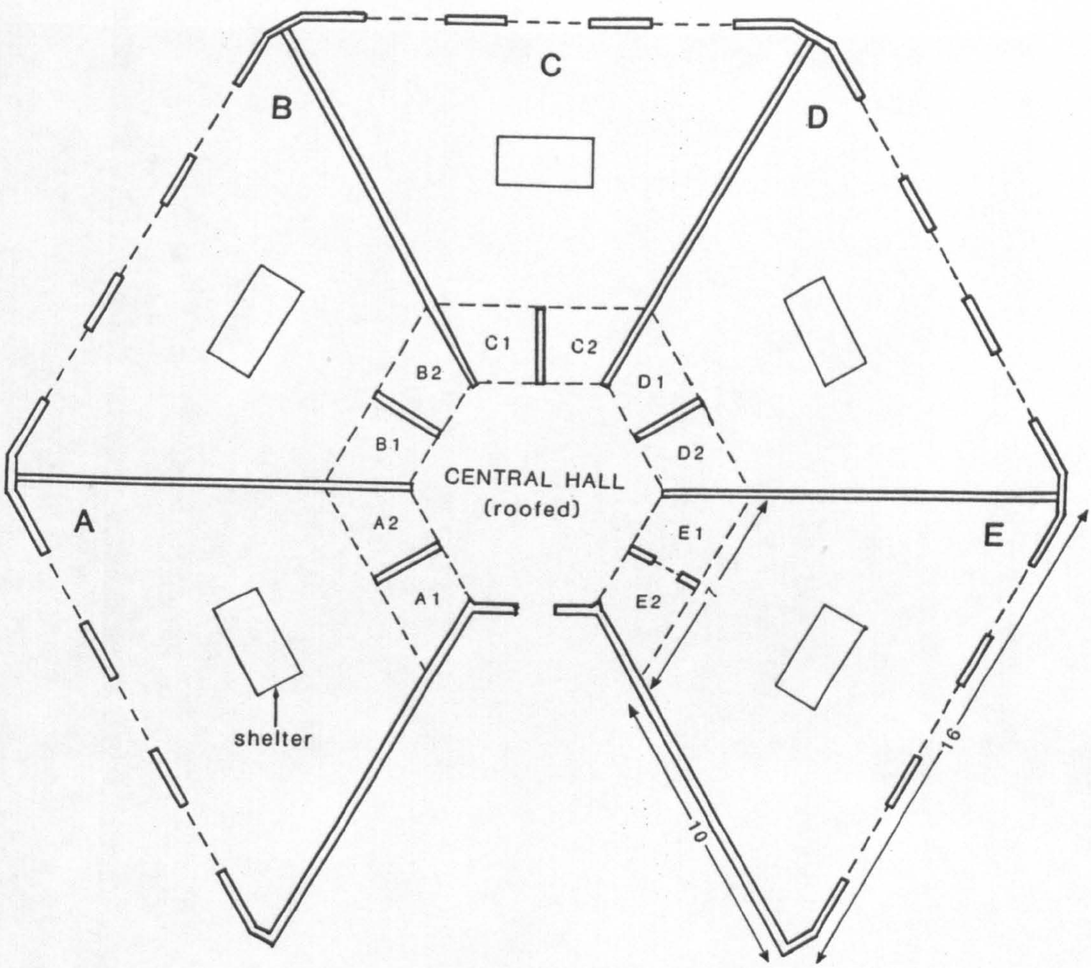


**FIGURE 2.2** Diagram of Vilab outdoor enclosures from above.




solid lines indicate concrete walls

broken lines indicate steel bars (10 cm apart)

measurements are in metres

**FIGURE 2.3** Chimpanzees in Vilab outdoor enclosure.

Seven members of Group 2 collecting food (bananas, pineapples, and sugar cane) from around the enclosure at feeding time.

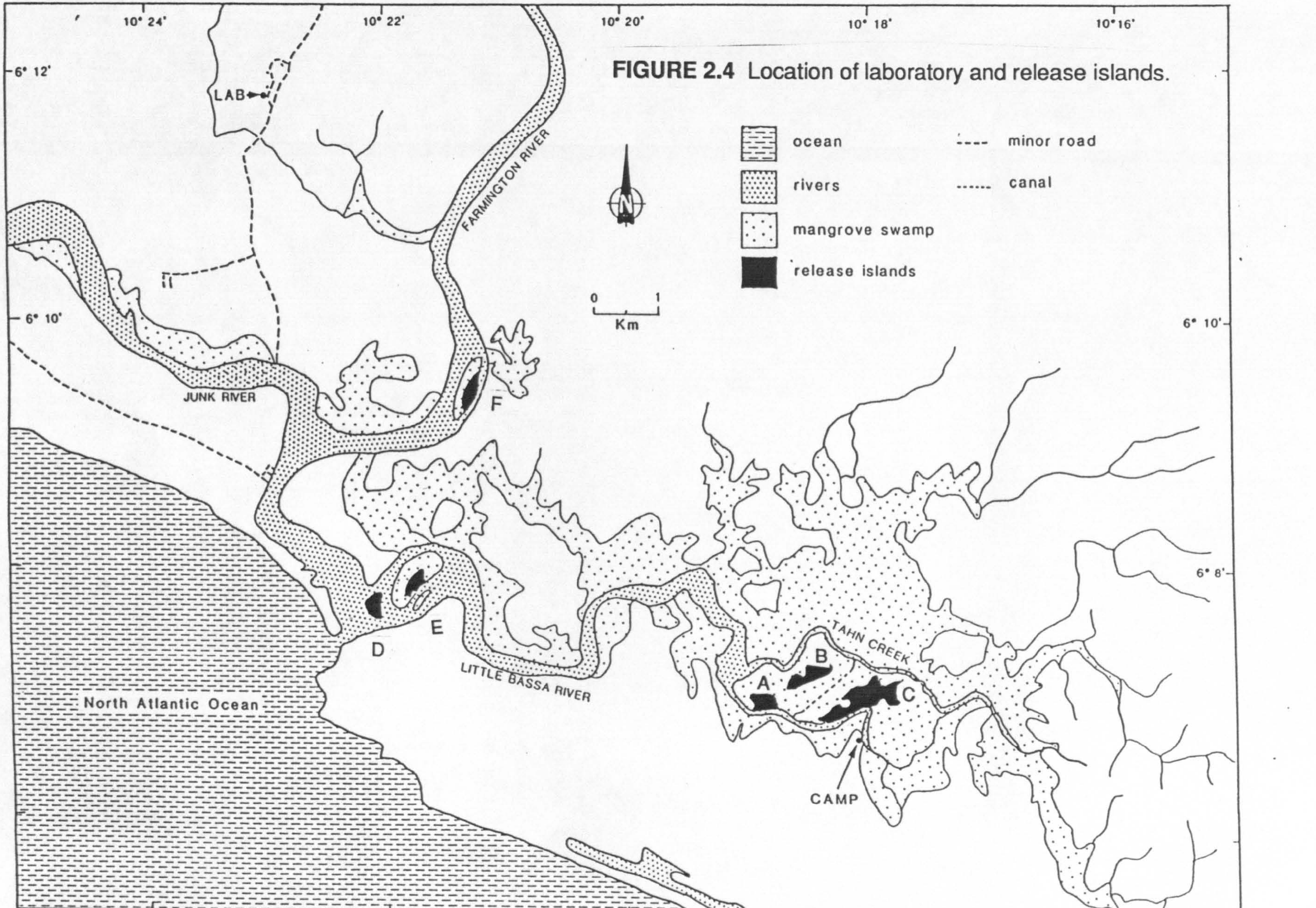



**FIGURE 2.4** Location of laboratory and release islands.

through mangrove between Islands A and C and meeting.

Both islands were completely forested with evergreen secondary forest. The species of tree so far identified are listed in Table 2.1 (HENTSCHEL, unpub.). Paths were cut on both islands to allow human access. No mammals were ever seen on the islands, although footprints thought to be of a civet (*Viverra civetta*) were once found. Crocodiles (*Crocodilia* spp.) were occasionally seen in mangrove areas on the mud at low tide and snakes were occasionally seen on the mainland opposite the islands and swimming in the river. Primates known to inhabit the mainland adjacent to the islands were Diana monkeys (*Cercopithecus diana*).

An area at the shore of Island A was cleared of vegetation; it covered $18m^2$ at high tide and $30m^2$ at low tide. Subjects could get drinking water here from a lixit which they controlled. This was also the area where they were given fruit and bread on provisioning days, and occasionally milk. Food was handed to individual chimpanzees by the author and laboratory staff. There was a cage at this site, measuring 3x2x1 m, constructed of wire mesh with a wooden floor and roof.

## SUBJECTS.

Subjects were 48 chimpanzees (*Pan troglodytes verus*), 20 males and 28 females, aged from 5 to over 20 years. Tables 2.2 and 2.3 list the subjects which are split into 2 groups : the first study group (Group 1), and later additions to it (Group 2). The groups in which subjects were kept are discussed in relevant sections. All subjects were wild-born and had spent up to 15 years in captivity.Some subjects had been kept solitarily as pets for up to 7 years before being kept together with other chimpanzees.

## DATA COLLECTION.

i) Laboratory. While the animals were in captivity data were collected mainly with the use of check sheets on a clip-board, but occasionally by dictating observations onto a tape-recorder and later transcribing, or by taking *ad libitum* notes. The times when these methods were used are mentioned where appropriate. Two types of check sheet were used. First a `group scan sheet' was used to simultaneously record general behavioural categories for all members of a sub-group. This type of check sheet was used for groups

**TABLE 2.1** Species of trees so far found on Islands.

| Species | Isl. A | Isl. B | Isl. C | Released chimp. food (pers. obs.) | Wild chimp. food (see below) |
|---|---|---|---|---|---|
| *Albizia zygia* | | | + | | √ |
| *Anthocleista nobilis* | + | + | + | | |
| *Cassipourea nialatou* | | | + | | |
| *Danielia thurifera* | | | + | | |
| *Elaeis guineensis* | + | + | + | √ | √ |
| *Haplomorosa monophylla* | + | + | + | | |
| *Oldfieldia africana* | + | | + | | |
| *Parinari excelsa* | + | + | + | √ | √ |
| *Pentadesma butyracea* | | + | + | | * |
| *Sacoglottis gabonensis* | + | + | + | | √ |
| *Samanea dinklagei* | + | | | | |
| *Symphonia globulifera* | | | + | | |
| *Tarrieta utilis* | | | + | | |
| *Tetraberlinia tubmaniana* | + | | | | |
| *Uapaca heudelotti* | | + | + | | * |

+ = species recorded on Island
√ = positive evidence of species being eaten
* = possible chimpanzee food (other species from same genus eaten elsewhere)

Island species data are from HENTSCHEL (unpub.).

Wild chimpanzee food data are from BOESCH & BOESCH (1984), SUGIYAMA & KOMAN (1987), WRANGHAM (1975), and WILLIAMSON (pers. comm., data from Lopé Reserve, Gabon).

TABLE 2.2 Subject Group 1. Group 1 is split into sub-groups a,b,and c according to caging (enclosure A, B, or D). Sub-group d includes subjects who were added to the above sub-groups to form a larger island release group. All measures are in years. Subjects are listed alphabetically within sub-groups.

| | Name | Sex | Age at Capture | Age on Release | Period in Captivity | Pet For | Date Added | Date Released |
|---|---|---|---|---|---|---|---|---|
| a) | Daniel | m | 0.5 | 10.5 | 10.0 | 5 | | 13/8/85 |
| | Hardtimes | f | 1.0 | (10.5) | 9.0 | 0 | | - |
| | Maki | f | 0.5 | 9.5 | 9.0 | 0 | | 20/7/85 |
| | Ms. Fields * | f | 1.0 | (11.5) | 9.0 | 7 | | - |
| | Putukin * | f | 1.0 | (9.5) | 9.0 | 0 | | - |
| | Samantha | f | 1.0 | 9.5 | 8.5 | 0 | | 20/7/85 |
| | Sokomodo | m | 2.0 | 9.5 | 7.5 | 1 | | 13/8/85 |
| b) | Brutus | m | 1.0 | 8.5 | 9.5 | 3 | | 13/8/85 |
| | DmW | f | 1.5 | 8.5 | 7.0 | 4 | | 22/6/85 |
| | Hemaphrodite | m | 0.75 | 5.5 | 4.75 | 0.25 | | 7/6/85 |
| | Helen | f | 1.0 | 5.5 | 4.5 | 0.5 | | 7/6/85 |
| | Maria | f | 1.5 | 6.5 | 5.0 | 0.5 | | 7/6/85 |
| | Trokon | m | 0.5 | 8.5 | 8.0 | 3 | | 7/6/85 |
| c) | Carolla | f | 2.5 | 9.5 | 7.0 | 1 | | 22/6/85 |
| | Ginger * | m | 1.0 | (11.5) | 10.0 | 7 | | - |
| | Goldilocks | f | 2.5 | 7.0 | 4.5 | 0.5 | | 22/6/85 |
| | Houdina | f | 3.0 | 9.5 | 6.5 | 4 | | 22/6/85 |
| d) | Blamah | f | 1.5 | 7.5 | 6.0 | 0.5 | 4/85 | 7/6/85 |
| | Cruella | f | 3.0 | 7.0 | 4.0 | 0 | 5/85 | 7/6/85 |
| | Franco ** | m | 1.0 | 9.5 | 8.5 | 4 | 4/85 | 7/6/85 |
| | Grace | f | ? | > 20.0 | >15.0 | 0 | 5/85 | 20/7/85 |
| | Knut ** | m | 2.0 | 6.5 | 4.5 | 1 | 4/85 | 7/6/85 |
| | Meryn | m | 0.5 | 5.0 | 4.5 | 0 | 4/85 | 7/6/85 |
| | Pim | m | 2.0 | 5.0 | 3.0 | 0 | 5/85 | 7/6/85 |
| | Popeye | f | ? | 6.5 | ? | <1 | 5/85 | 7/6/85 |
| | Reagan | m | 3.0 | 7.5 | 4.5 | 0 | 4/85 | 7/6/85 |
| | | 11m 13f | x = 1.56 | x = 8.29 | x = 6.75 | x = 1.37 | | |

* - not released
** - Franco, Reagan and Knut originally came from sud-group b.
? - unknown
x - calculated only for subjects released, and for whom data are available.

TABLE 2.3 Subject Group 2. Group 2 is split into sub-groups according to date added to Group 1. All measures are in years. Subjects are listed alphabetically within sub-groups.

| | Name | Sex | Age at Capture | Age on Release | Period in Captivity | Pet For | Date Added | Date Released |
|---|---|---|---|---|---|---|---|---|
| a) | Anita | f | 2.0 | 7.0 | 5.0 | 0.17 | 2/86 | 11/6/87 |
| | Bertha | f | 0.5 | 6.5 | 6.0 | 1.0 | 2/86 | 8/6/87 |
| | Bill | m | 0.5 | 7.0 | 6.5 | 1.5 | 2/86 | 8/6/87 |
| | David | m | 1.0 | 9.0 | 8.0 | 0.17 | 2/86 | 17/6/87 |
| | Mabel | f | 1.5 | 6.5 | 5.0 | 0.17 | 2/86 | 3/6/87 |
| | Moffit | f | 1.5 | 6.5 | 5.0 | 0 | 2/86 | 8/6/87 |
| | Natasha | f | 3.0 | 7.0 | 4.0 | 0 | 2/86 | 11/6/87 |
| | Tipsy | f | 1.5 | 6.5 | 5.0 | 0.25 | 2/86 | 8/6/87 |
| | Tolkien | m | 2.0 | 6.5 | 4.5 | 0.17 | 2/86 | 8/6/87 |
| | Twebo | f | 1.5 | 7.0 | 5.5 | 0 | 2/86 | 8/6/87 |
| b) | Bahnti | f | 2.5 | 5.5 | 3.0 | 0.25 | 5/86 | 8/6/87 |
| | Big Sore | f | 4.0 | 8.0 | 4.0 | 1.0 | 5/86 | 3/6/87 |
| | Dr. Me | m | 1.5 | 5.0 | 3.5 | 1.0 | 5/86 | 8/6/87 |
| | Gunter * | m | 0.5 | * (6.0) | 5.0 | 5.0 | 7/86 | - |
| | Telle | f | 1.5 | 6.5 | 5.0 | 0.6 | 5/86 | 3/6/87 |
| | Wolfram | m | 2.5 | 6.0 | 3.5 | 1.5 | 5/86 | 3/6/87 |
| c) | Jimbo ** | m | 1.0 | 7.5 | 6.5 | 5.5 | 11/86 | 11/6/87 |
| | Mango | m | ? | 9.5 | ? | 0 | 11/86 | 11/6/87 |
| | Saffa | m | 2.0 | 8.0 | 6.0 | 0.25 | 12/86 | 3/6/87 |
| | | 9m<br>10f | x = 1.76 | x = 6.97 | x = 5.06 | x = 0.75 | | |

* - not released
** - released and returned to lab on day 1 (see text)
? - unknown
x - calculated only for subjects released, and for whom data are available.

of up to 7 members. This was used to during the first 3 months of laboratory observations, when the largest sub-group contained 7 members. Thereafter, when new group members were added to these sub-groups, focal subject check sheets were used (see below). Group scan sheets were used to record mainly social behaviour - aggression, grooming, social play, and sexual behaviour (see Appendix A for definitions), but also to record stereotyped or abnormal behaviour. Sampling was on 1 minute intervals for 20 minute periods, a metronome bleeper with earplug being used for timing. Behaviour was sampled in 2 ways, depending on bout-length. Longer-lasting behavioural categories which spanned intervals of more than 1 minute were recorded using *instantaneous sampling* (ALTMANN, 1974; MARTIN & BATESON, 1986), that is the behaviour was recorded on 1-minute intervals. Categories recorded in this way were grooming, social play, and stereotyped behaviour. Categories of behaviour which occurred infrequently and briefly were recorded using *one-zero sampling* ( ALTMANN, 1974; MARTIN & BATESON, 1986), that is the behaviour was recorded as being present or absent at any time during a 1-minute interval. Behaviours recorded in this way were aggression and sexual behaviour. Also, on 5-minute intervals spacing data were recorded. Individuals were recorded as being solitary, in proximity (at less than i m from another individual), or in contact (with any part of an individuals body touching another individual). In the first period of observations (February - May 1985) the 3 sub-groups being studied were small enough to use group scan sheets. Later, when transfers were made between groups and additions were made to groups, focal subject check sheets were used, that is sampling was focused on 1 individual of the group at a time in random order. The same categories as above were used, but were now only recorded when they involved the focal individual. Spacing data for all sub-group members were recorded on 5-minute intervals as before.

ii) Island. Following the release of the study group onto Island A, data were recorded on an *ad libitum* basis rather than with check sheets. There were 2 reasons for this : First, because the chimpanzees could now come into contact with the author, this made it difficult to work with equipment such as a metronome bleeper and a clip board with a check sheet, as inquisitive animals tried to investigate, and in some cases to take these equipment away from the author. The author therefore worked with minimal equipment : a small notepad with a pencil attached with a piece of string. The other reason for not using focal subject check sheets was that for the authors own safety it was better to stay alert to what was happening in the group as a whole rather than to focus attention on 1 individual alone. When in the interior of the island and among the whole group it was prudent to scan continually, watching all individuals and looking out for potentially aggressive interactions, which might lead to an aggressive display by the older males of the group. In such situations, displaying males sometimes began to display towards humans nearby. Awareness of impending aggression allowed humans present to stand up (if previously seated) and to move the the edge of the group, reducing the possibility of being caught in the middle of an aggressive interaction between group members.

SAMPLING PROBLEMS

i)Laboratory. Sampling was carried out between 8.00 and 17.00 hours, sampling sessions being evenly distributed throughout the working day. Scheduled feeding times (between 10.30 and 11.00, and between 2.30 and 3.00) were avoided, as were scheduled laboratory procedures, such as cleaning of the cages at the rear of an enclosure or removal of subjects from an enclosure. Cleaning procedures were the least disruptive and had to be avoided only when the cages of an enclosure under observation were being cleaned. Removal of sub-group members was more disruptive, particularly if it involved the sub-group under observation. Even when it involved a group in another enclosure, observation still had to be avoided because all groups in the outdoor enclosures became excitable and watched procedures being carried out with other groups through the central area of the building. During the first period of observations at the laboratory (Feb-May 1985), there were few occasions when removal of sub-group members occurred, but following this period a group of chimpanzees (not in this study) involved in an ongoing experiment were housed in 1 enclosure, and group members frequently had to be separated. These procedures disrupted the groups in all the other enclosures, including sub-groups from this study, which were therefore not observed during these times.

Throughout the period of data collection there were changes in the composition of the sub-groups. When removals from sub-groups were only temporary and brief (for example, 1 group member for 1 day), observations were discontinued until the individual was returned to the group. If an individual was removed for longer, however, observations continued as normal.

ii)On Island. Sampling was carried out between 8.00 and 18.00 hours. Sampling began from the time the observer arrived at the island and continued until departure, and was carried out unless the author was involved in another activity, such as giving food to the subjects or using radio-telemetry equipment (see below) to find a missing subject. When subjects were first released the author went to the island every day, but after 1 month when the number of feeding days was reduced, the author could only go to the island on scheduled feeding days, or when at least 1 member of the laboratory staff was available to accompany the author.

The differences in sampling techniques used at the laboratory compared with the island, for example, check sheets on focal subjects compared to *ad libitum* notes, limits the possibility of direct quantitative comparison of laboratory and island data.

## CHRONOLOGY OF EVENTS

Throughout the study period from February 1985 to July 1987 there were many changes in the study group's location and composition. The main reason for changes in group location was that when the canal separating Islands A and C (Figure 2.4) became too shallow in the dry season, the chimpanzees on these islands could cross the canal, which could result in serious fighting between the 2 groups. The study group was therefore transferred from Island A to the laboratory or to another island during dry seasons.

There were various reasons for changes in group composition : laboratory procedures (which could lead to additions or removals), illness and deaths, and removals due to incompatability with other group members. Also group members who were very aggressive to humans (such as attempting to bite humans at any opportunity) were removed from the group because follow-up of the group was planned after release onto the island which meant contact between humans and chimpanzees. The changes in group location and composition throughout the study period are summarized in Figure 2.5. They can generally be split into the following sections :

1)Lab. Study Period 1 (February1985 - June 1985)

During this period sub-groups a-c of Group 1 (Table 2.2) were studied in each of their enclosures at the laboratory (Figure 2.6). In April and May 1985, some members were transferred among these 3 sub-groups, the members of Group 1d were introduced,

**FIGURE 2.5** Changes in study group location and composition throughout study period.

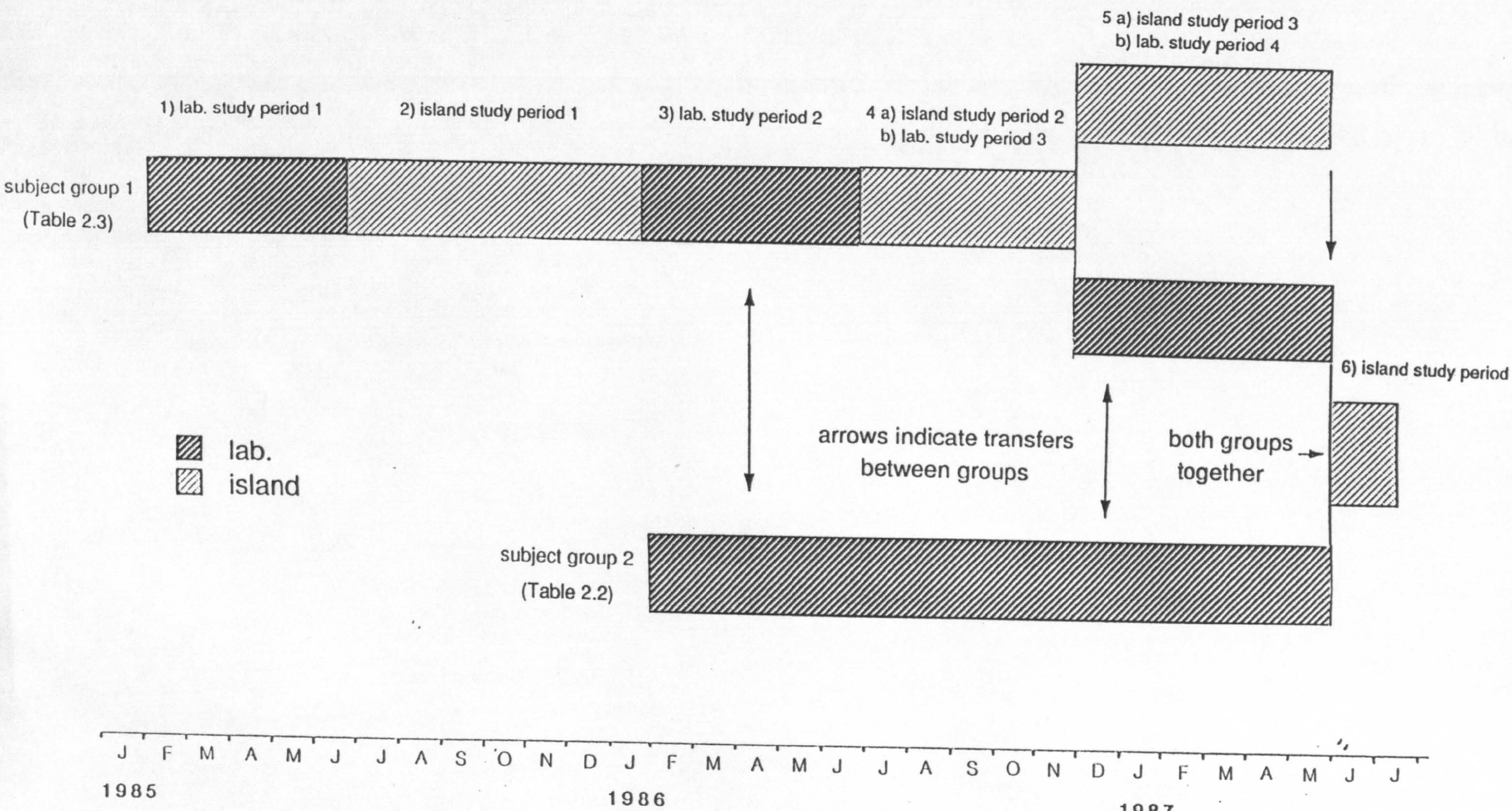
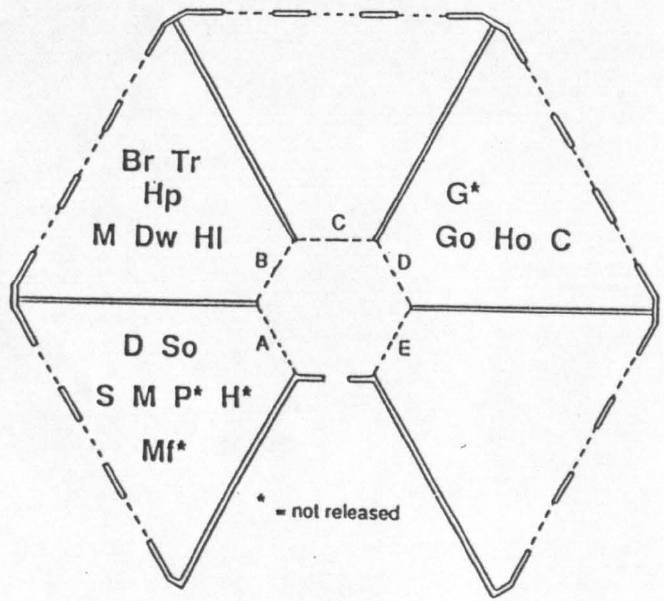


**FIGURE 2.6** Location of members of Group 1 (a-c) in April, 1985.




Enclosure A

males : D-Daniel
So- Sokomodo
females : H-Hardtimes
M-Maki
Mf-Miss Fields
P-Putukin
S-Samantha

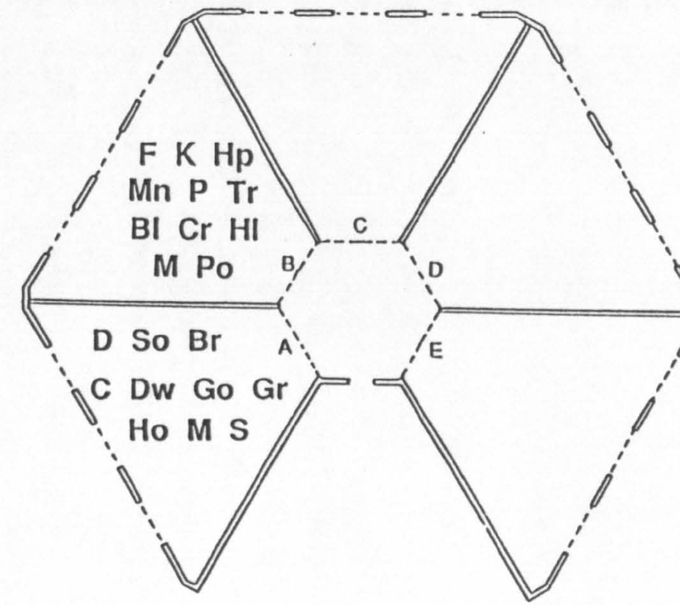
Enclosure B

males : Br-Brutus
Hp-Hermaphrodite
Tr-Trokon
females : Dw-DmW
Hl-Helen
M-Maria

Enclosure D

male : G-Ginger
females : C-Carolla
Go-Goldilocks
Ho-Houdina

**FIGURE 2.7** Location of members of Group 1 (a-d) in May, 1985.




Enclosure A

males : D-Daniel
So-Sokomodo
Br-Brutus
females : C-Carolla
Dw-DmW
Go-Goldilocks
Gr-Grace
Ho-Houdina
M-Maki
S-Samantha

Enclosure B

males : F-Franco
K-Knut
Hp-Hermaphrodite
Mn-Meryn
P-Pim
Tr-Trokon
females : Bl-Blamah
Cr-Cruella
Hl-Helen
M-Maria
Po-Popeye

and subjects not scheduled for release were removed from the sub-groups. All subjects were then housed in 2 separate enclosures until their release (Figure 2.7).

2) Island Study Period 1 (June 1985 - November 1985)

Begining on 7 June 1985, members of subject group 1 were released onto Island A. They were released in 4 sub-groups, with the last sub-group being released on 6 August 1985. The group was then studied until the end of November 1985. In January 1986, during a period when the author was away, an adolescent male (*Hermaphrodite*) from the Island A group crossed the canal between Islands A and C and was killed by chimpanzees on Island C. The rest of the Island A group was then returned to the laboratory to prevent any further group members crossing to Island C.

3) Lab Study Period 2 (February 1986 - June 1986)

From February 1986 until June 1986 Group 1 was returned from Island A and remained at the laboratory. During this period members of Groups 2a and 2b were added (Figures 2.8 - 2.10). These new group members were to be released in June 1986 when the Group 1was returned to Island A, but because there were no radio-transmitter collars available at that time, the new group members remained at the laboratory when Group 1 was released onto Island A for the second time.

4a) Island Study Period 2 (June 1986 - November 1986)

In June 1986, the 12 chimpanzees ofGroup 1 who had been on Island A (from June 1985 until January 1986), and then returned to the laboratory, were again released onto Island A. They were studied on Island A until their transfer in November 1986.

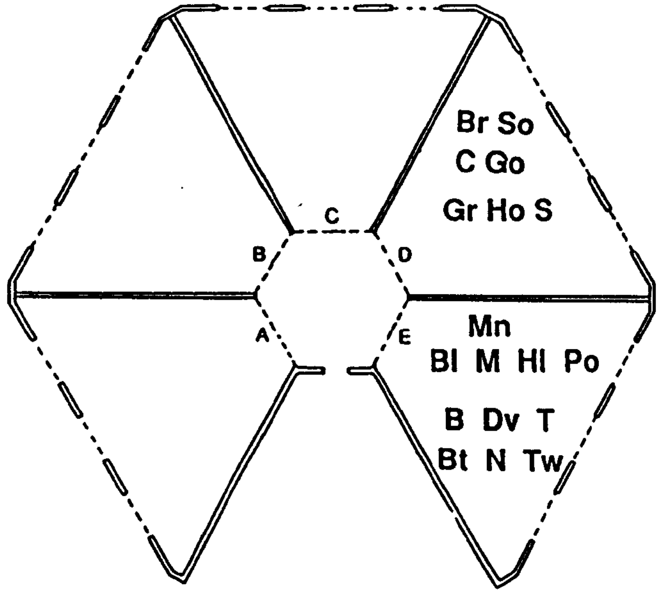
b) Lab. Study Period 3 (June 1986 - November 1986)

When the members of Group 1 were returned to Island A, the members of Group 2 continued to be studied at the laboratory. They were kept together for most of this time, until the group became too large to keep in 1 enclosure, and they were split into 2 sub-groups, with transfers occurring between the 2 sub-groups occasionally.

5a) Island Study Period 3 (December 1986 - June 1987)

From the end of November 1986, 5 members of Group 1 (*Brutus, Goldilocks, Popeye, Samantha, Sokomodo*) spent 6 months on a 6 ha island (Island E, Figure 2.4). They were observed for short periods after each daily feeding, but not studied as

FIGURE 2.8 Location of Group 1 (returned from island) and Group 2 (a & b) in February, 1986.




Enclosure D :

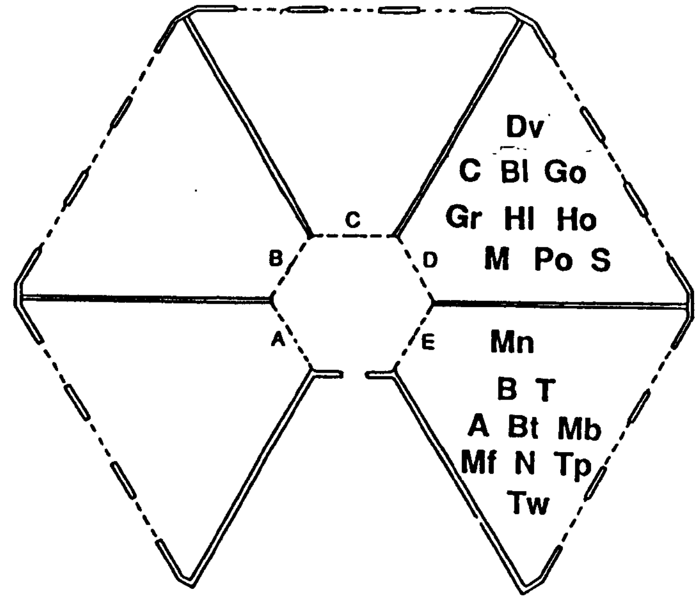
males : Br - Brutus
So - Sokomodo
females : C - Carolla
Go - Goldilocks
Gr - Grace
Ho - Houdina
S - Samantha

Enclosure E :

Subject group 1 ; male : Mn - Meryn
females : Bl - Blamah
M - Maria
Hl - Helen
Po - Popeye

Subject group 2 ; males : B - Bill
Dv - David
T - Tolkein
females : Bt - Bertha
N - Natasha
Tw - Twebo

FIGURE 2.9 Location of Group 1 and Group 2 (a & b) in April, 1986.




Enclosure D :

male : Dv - David (SG2)
females (all SG1) : C - Carolla
Bl - Blamah
Go - Goldilocks
Gr - Grace
Hl - Helen
Ho - Houdina
M - Maria
Po - Popeye
S - Samantha

Enclosure E :

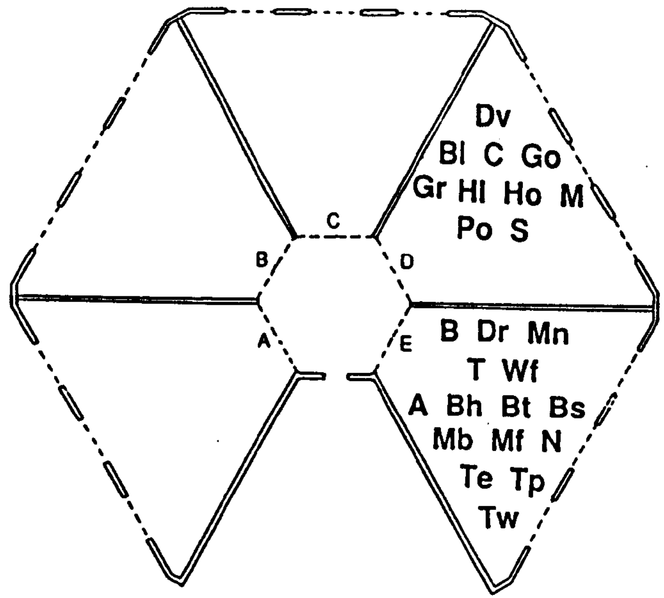
(from subject group 2 unless stated otherwise)

males : B - Bill
Mn - Meryn (SG1)
T - Tolkein
females : A - Anita
Bt - Bertha
Mb - Mabel
Mf - Moffit
N - Natasba
Tp - Tipsy
Tw - Twebo

SG1 = subject group 1
SG2 = subject group 2

Brutus and Sokomodo were each in individual (but connected) cages. They were removed from the group because they were being so aggressive towards the females.

**FIGURE 2.10** Location of Groups 1 & 2 in June, 1986.




Enclosure D :

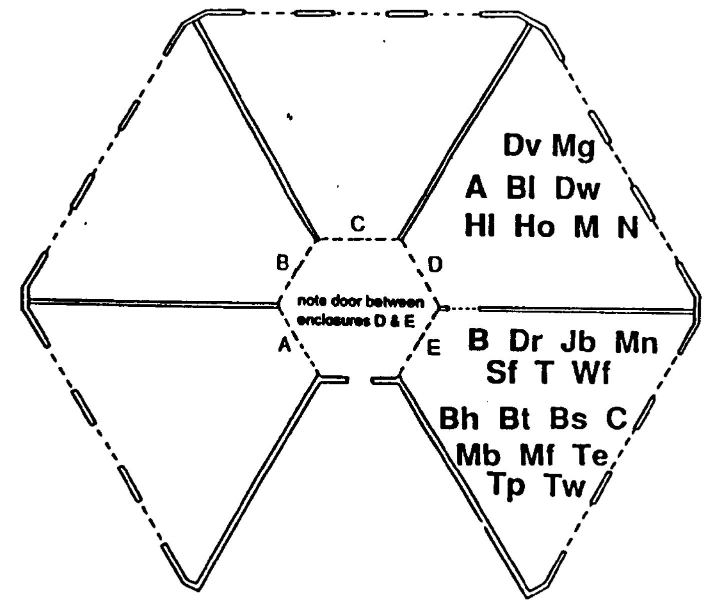
male : Dv - David (SG2)
females : Bl - Blamah
(all SG1) C - Carolla
Go - Goldilocks
Gr - Grace
Hl - Helen
Ho - Houdina
M - Maria
Po - Popeye
S - Samantha

SG1 = subject group 1
SG2 = subject group 2

Enclosure E :

males : B - Bill (SG2)
Dr - Dr. Me (SG2)
Mn - Meryn (SG1)
T - Tolkein (SG2)
females : A - Anita
(all SG2) Bh - Bahnti
Bt - Bertha
Bs - Big Sore
Mb - Mabel
Mf - Moffit
N - Natasha
Te - Telle
Tp - Tipsy
Tw - Twebo

**FIGURE 2.11** Location of Groups 1 & 2 in May, 1987.




Enclosure D :

males : Dv - David (SG2)
Mg - Mango (SG2)
females : A - Anita (SG2)
Bl - Blamah (SG1)
Dw - DmW (SG1/2) *
Hl - Helen (SG1)
Ho - Houdina (SG1)
M - Maria (SG1)
N - Natasha (SG2)

SG1 = subject group 1
SG2 = subject group 2

Enclosure E :

(from subject group 2 unless otherwise stated)

males : B - Bill
Dr - Dr Me
Jb - Jimbo
Mn - Meryn (SG1)
Sf - Saffa
T - Tolkein
Wf - Wolfram
females : Bh - Bahnti
Bt - Bertha
Bs - Big Sore
C - Carolla (SG1)
Mb - Mabel
Mf - Moffit
Te - Telle
Tp - Tipsy
Tw - Twebo

* DmW was originally a member of subject group 1, but was removed from the group and returned later when members of subject group 2 were being introduced.

intensively as before.

b) Lab Study Period 4 (December 1986 - June 1987)

From November 1986 until June 1987, the members of Group 1 who had been returned from Island A were re-introduced to the members of Group 2. All subjects were housed in enclosures D & E, but could see and interact with one another because a barred door had been inserted in the wall separating enclosures D & E (Figure 2.11). In May 1987 this door was opened and all 25 subjects could freely move between the 2 enclosures.

6. Island Study Period 4 (June 1987 - July 1987)

In June 1987, Groups 1 & 2 were released together on Island A. This was the first release for the members of Group 2. Their reactions to release and their interactions with members of Group 1 were studied until July 1987.

## STATISTICS

Statistical tests were calculated by computer using the SPSSX statistical package (SPSS Inc., 1966). Non-parametric statistical tests were used (SIEGEL, 1956). Tests were two-tailed unless otherwise stated. Level of significance was $p = 0.05$.

# CHAPTER 3

## BEHAVIOUR BEFORE RELEASE

### SOCIAL LIFE BEFORE RELEASE

Some studies have presented data which indicates that a change in environment can produce changes in social behaviour among groups of chimpanzees (NIEWENHUIJSEN & de WAAL, 1982; CLARKE et al., 1982). Such data are not available for previous studies which have involved releasing captive chimpanzees into natural environments, however (GRZIMEK, 1970; BREWER, 1982; CARTER, 1981, 1988). In the present study, data were collected on social behaviour of chimpanzees for at least 4 months before release, which could then be compared with data on social behaviour after release onto Island A.

#### Sub-Group Social Structure

As a measure of sub-group social structure, data on spacing of individuals in each sub-group were collected. Each individual was recorded as being solitary, in proximity, or in contact with other individuals, with their identities being recorded. These data were collected to show if there were trends in spacing which indicated individual preferences in choice of companions. These data are listed in Appendix B, and are illustrated in figures in the following sections.

a) Solitary Data

Solitary data for members of Group 1 are presented in Figures 3.1 and 3.2. The percentage of samples each individual was recorded as solitary varies from 17 % (*Samantha*) to 74 % (*Trokon*). There is no significant difference between the mean value for males and females (Mann-Whitney U-test, $z = -1.2$, $p = 0.23$). The 2 individuals who were markedly more solitary were *Trokon* and *Goldilocks*, who were also the 2 subjects who showed most stereotyped behaviour in these sub-groups (see p. 166).

The amount of samples in which a subject was recorded as solitary varied as the group composition changed. This is illustrated in Figure 3.3. In this the case the oldest male and female of the group in enclosure B had been transferred to enclosure A and

**FIGURE 3.1** Solitary data before release, Group 1 (a-c).

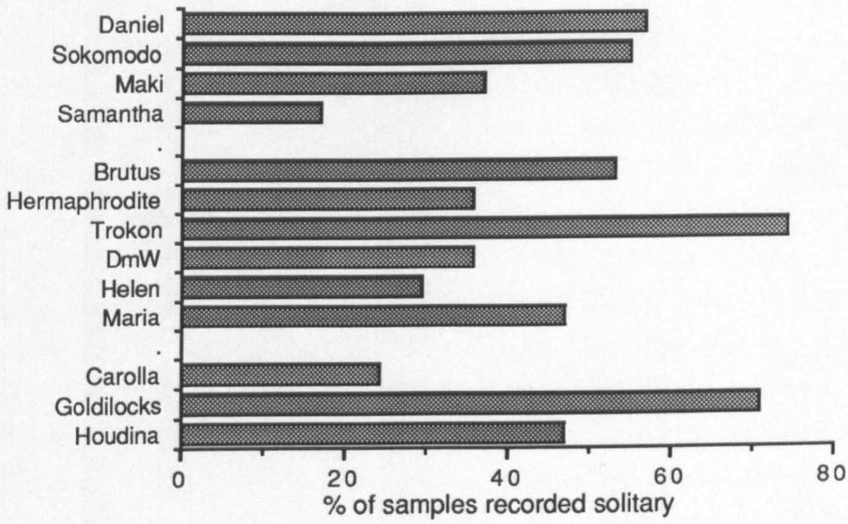
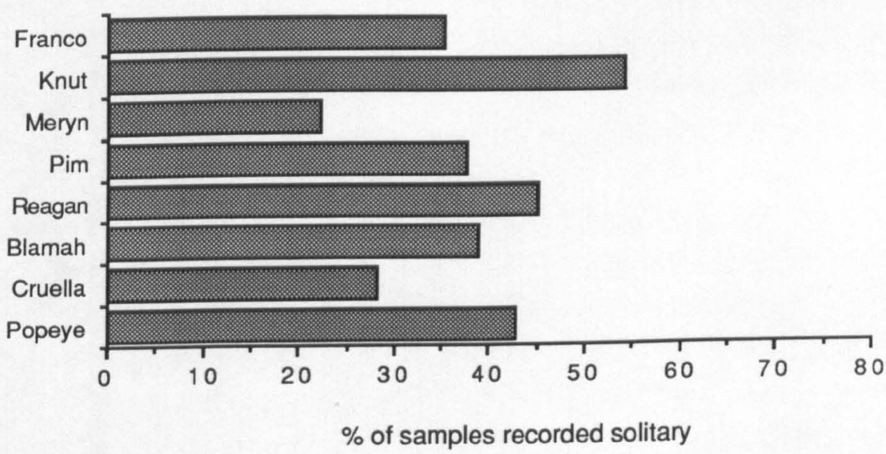



**FIGURE 3.2** Solitary data before release, Group 1(d).




Males then females are listed alphabetically within sub-groups.

new, younger group members were added (see Figures 2.6 and 2.7). Spatial data of the 4 group members who were not transferred could be compared before and after the change in group composition. In Figure 3.3, a decrease in the percentage of samples in which they were recorded as solitary is evident for all 4 subjects, which would be expected as there were 11 subjects caged in the same area which previously contained only 6. The decrease in solitary scores are not significant for *Hermaphrodite* and *Helen*, but are highly significant for both*Trokon* (Wilcoxon test, z = -3.7.p < 0.01, 2-tailed) and *Maria* (Wilcoxon test, z = -3.7, p < 0.01, 2-tailed). *Trokon* showed stereotyped behaviour, usually when he was not involved in other activities such as eating, grooming, and playing. Following additions of new, younger group members who played more frequently (see below) *Trokon* therefore had more opportunity to take part in an activity other than solitary stereotyped behaviour. The difference in *Maria's* solitary scores is probably due to the removal of the previous alpha male *Brutus*. *Brutus* frequently attacked *Maria* and she therefore avoided him, which often meant she was also avoiding other group members in proximity to *Brutus* (eg. if *Brutus* and other group members were in the shelter, *Maria* did not enter it). Following *Brutus'* removal, however, when *Maria* was no longer a target of aggression, she spent more time in proximity with the other group members.

Solitary data for Group 2 (with 1 member of Group 1) are illustrated in Figures 3.4 and 3.5. Solitary scores range from 16 % (*Meryn*; Group 1) to 47 % (*Bill*) in Figure 3.4, and from 18 % (*Bahnti*) to 57% (*Wolfram*) in Figure 3.5. The average of these scores is lower than that for Group 1 scores, which would be expected given that more subjects were caged together in the same area.When members of Group 2b were added to members of Group 2a (Figure 3.5), there was a trend for an increase in solitary scores for some subjects, despite the increase in numbers of subjects, but overall the increase in solitary scores was not significant (Wilcoxon test, z = -1.5, p = 0.12). The 2 subjects with the highest solitary scores in Group 2, *Bill* and *Wolfram*, were the only 2 subjects who showed stereotyped behaviour, which was similar to the situation in Group 1, with *Goldilocks* and *Trokon* who showed most stereotyped behaviour (see p. 166).

The 3 members of Group 2c (*Jimbo, Mango*, and *Saffa*) were added to the prospective release group later than other subjects in Group 2 (Nov. - Dec. 1986), and for the 5 months they were studied before release many changes in sub-group composition occurred. In order to give some comparison of their solitary scores with those of other subjects, however, data from 2-3 months when sub-group composition

**FIGURE 3.3** Solitary data for members of Group 1 (b) who were studied before and after addition of new group members.

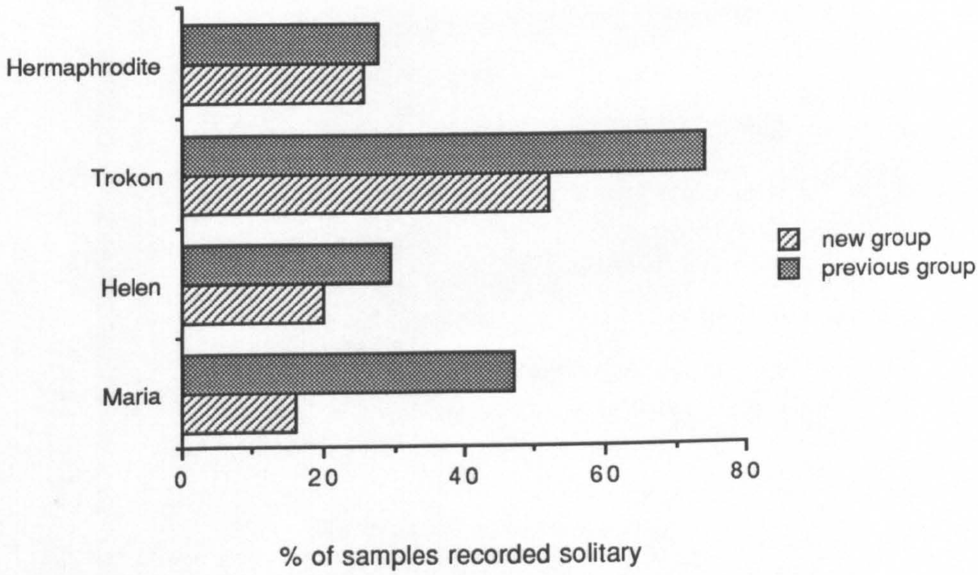
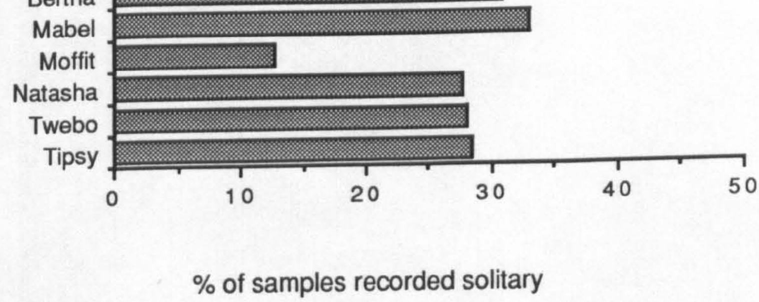
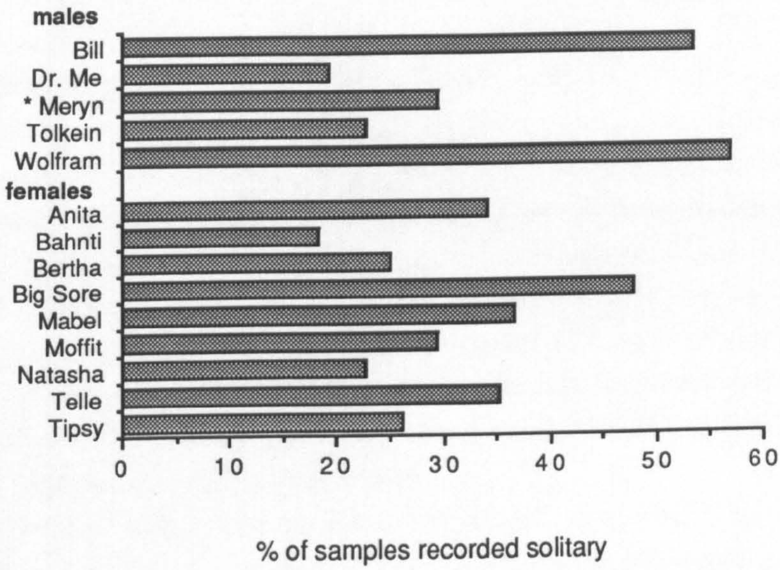



**FIGURE 3.4** Solitary data, Group 2 (a).



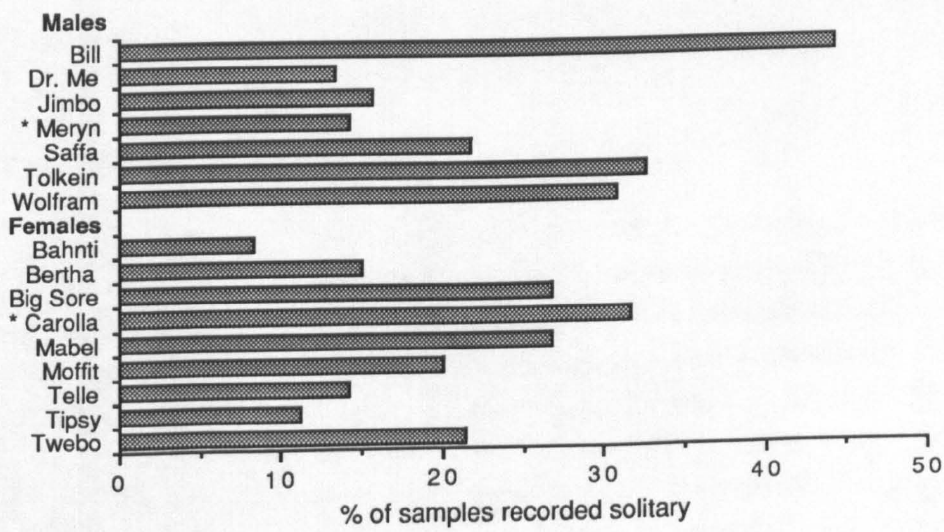

From data collected beween February and April, 1986. David's data are taken from only 5 hours of observation, then he was transferred to another enclosure becaause he was being so aggressive. Other subjects' data are taken from 21 hours of observation.
*Meryn is from Group 1.

**FIGURE 3.5** Solitary data, Group 2 (a & b).




From data collected in June, 1986. Each subjects' data are taken from 7 hours of observation, with the exception of Bill and Mabel, who were transferred (to be introduced to a new group member) after 5 hours of observation.

**FIGURE 3.6** Solitary data, Group 2, March - May, 1987.




Data for Jimbo, Tipsy, and Twebo are taken from 3 hours of observation, othersubjects' data are taken from 10 hours of observation.

* Meryn and Carolla from Group 1.

was relatively stable are presented in Figure 3.6 for *Jimbo* and *Saffa*, and Figure 3.7 for *Mango*. *Jimbo* had little time of stability in any sub-group because he was often a target of aggression. He was attacked so often by the females of Group 1 (those listed in Figure 3.7) that he was transferred to enclosure E, to be with younger subjects (as listed in Figure 3.6). This was related to the fact that *Jimbo* had been kept as a pet for almost 7 years and did not have a very long period of socialization before introduction to these groups (see below). *Jimbo's* percentage solitary score is much lower than it would have been if he had been in a sub-group with older group members, but he was never able to stay in such a sub-group long enough for comparable data to be collected. *Jimbo's* problems in some sub-groups were probably related to his rearing history rather than to the fact that he was introduced at a later date, because *Mango* and *Saffa* did not have the same problems with being introduced later.

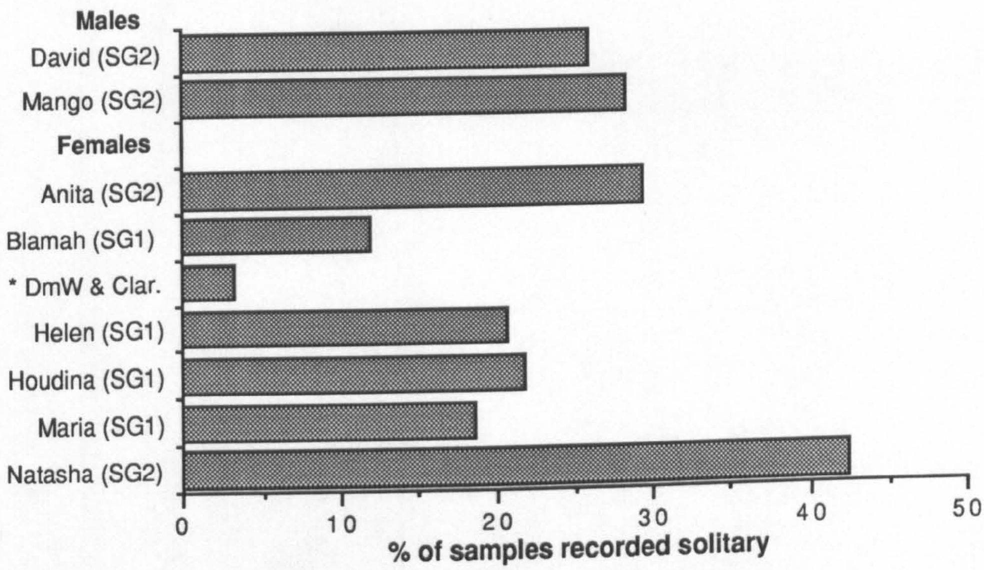
Some points should be made about Figure 3.7. First, *DmW's* very low percentage solitary score was due to the interest in her son, *Clarence*, who other subjects frequently groomed or played with. Also, even when *DmW's* score is not included, the solitary scores of the 4 members of Group 1 are much lower than that for the 4 members of Group 2 . These 4 females of Group 1 had now been together for over 2 years, and had formed a dominant sub-group, frequently jointly chasing or attacking members of Group 2 who had a lower status in this group. The difference in solitary scores may therefore reflect this difference in status, with the lower-ranking members of Group 2 avoiding members of Group 1, and thus spending a higher proportion of time alone.

## Proximity and Contact Data

Proximity and contact data for all subjects other than subject Group 2c are listed in Tables in Appendix B, and proximity data are illustrated in FIGURES 3.8 - 3.12. No 2 sub-groups have identical composition in terms of number of subjects or age/sex class, but some general points can be made. Figures 3.8 and 3.9 show a tendency for females to associate together more than males (Mann-Whitney U-test, $z = -2.0$, $p = 0.04$). The peripheral position of *Trokon* (Figure 3.9) corresponds with his high percentage solitary score and probably reflects how often he showed solitary stereotyped behaviour . The alpha male of subject group 1c, *Ginger* (Figure 3.10) was in proximity with one female of the group (*Carolla*) on more than 30 % of samples, but associated little with the other 2 females of this sub-group. *Ginger* often attacked these 2 females, particularly *Goldilocks*, who probably avoided him and was only recorded in proximity with *Ginger* on 9 % of

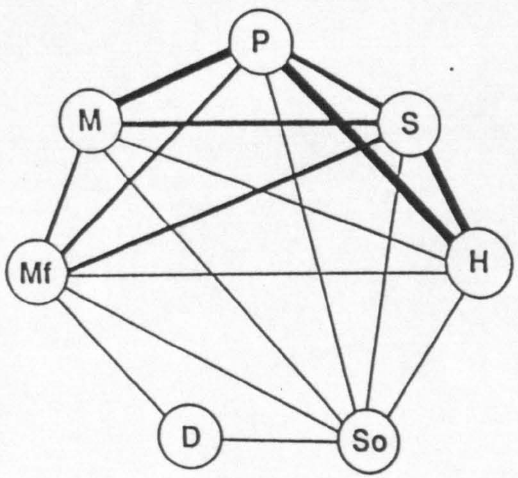
**Figure 3.7 Solitary data for some members of Groups 1 & 2, March -April, 1987.**

Data are taken from 8 hours of observation for each subject.




* DmW had a 16 month old son, Clarence, who was always in proximity or contact with her. They were therefore recorded together and DmW was only recorded as solitary if she was not near any adult or adolescent group members. Other group members, particularly the females, were very interested in Clarence and frequently groomed or played with him, which explains DmW's very low solitary score. In May, 1987, Clarence was removed from DmW and her solitary score rose to 25% of recorded samples. Note DmW was originally a member of subject group 1 (see text).

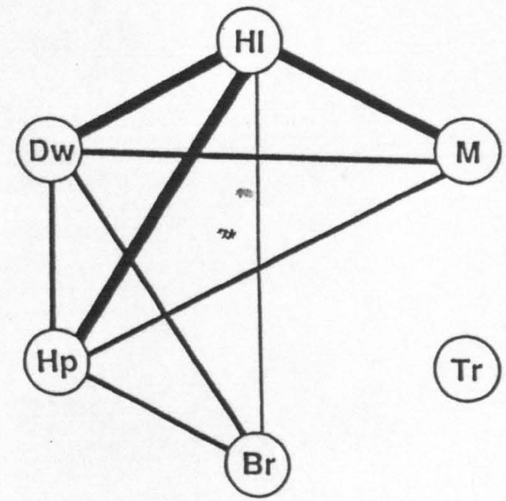
FIGURE 3.8 Proximity data, Group 1a.




* = not released

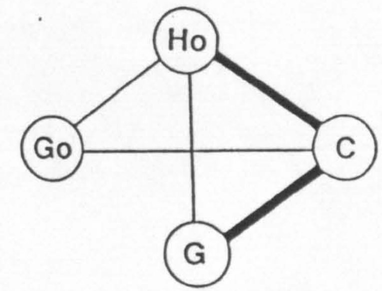
males : D - Daniel
So - Sokomodo
females : H - Hardtimes *
M - Maki
Mf - Miss Fields *
P - Putukin *
S - Samantha

FIGURE 3.9 Proximity data, Group 1b.




males : Br - Brutus
Hp - Hermaphrodite
Tr - Trokon
females : Dw - DmW
Hl - Helen
M - Maria

FIGURE 3.10 Proximity data, Group 1c.

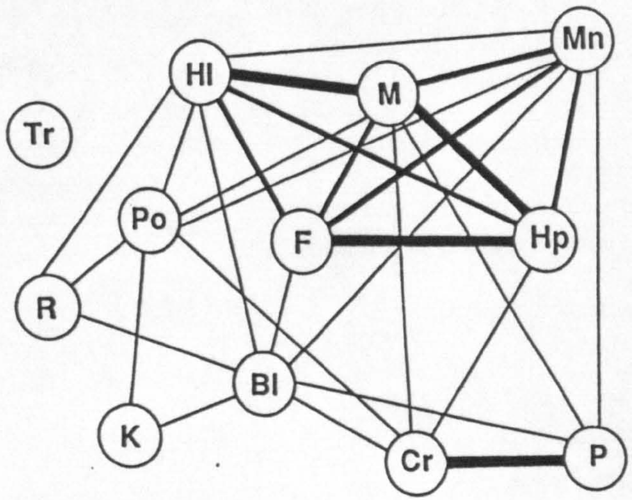



* = not released

male : G - Ginger *
females : C - Carolla
Go - Goldilocks
Ho - Houdina

width of lines is proportional to % of samples the individuals were recorded in proximity :

FIGURE 3.11 Proximity data, Group 1d (with some members of Group 1b).




* = member of sub-group 1d

males : F - Franco
Hp - Hermaphrodite *
K - Knut
Mn - Meryn
P - Pim
R - Reagan
Tr - Trokon *
females : Bl - Blamah
Cr - Cruella
Hl - Helen *
M - Maria *
Po - Popeye

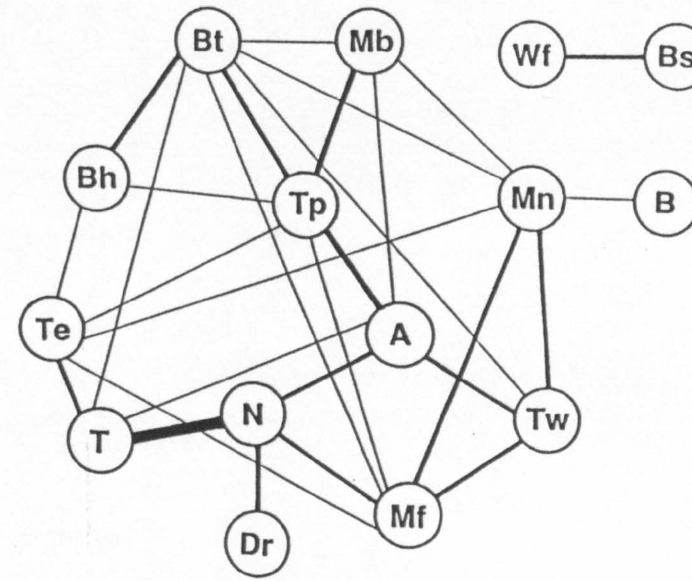
width of lines is proportional to % of samples the individuals were recorded in proximity :

> 10 %

> 20 %

> 30 %

FIGURE 3.12 Proximity data, Groups 2a & 2b.




males : B - Bill
Dr - Dr. Me
Mn - Meryn (SG1)
T - Tolkein
females : A - Anita
Bh - Bahnti
Bt - Bertha
Bs - Big Sore
Mb - Mabel
Mf - Moffit
N - Natasha
Te - Telle
Tw - Twebo

width of lines is proportional to % of samples the individuals were recorded in proximity :

≤ 7.5 %

> 10 %

> 30 %

SG1 = subject group 1

samples.

Figure 3.11 illustrates proximity data for a newly formed group. Four subjects were from Group 1b, and 8 from Group 1d (see Table 2.2). *Maria, Helen,* and *Hermaphrodite* remained closely associated and *Trokon* stayed on the periphery of the group as in Figure 3.9. Most of the members of Group 1d had not yet become very well integrated into the group, with the exception of *Franco*. *Franco* was the alpha male of this group and *Maria*, *Helen*, and *Hermaphrodite* associated with him, particularly *Hermaphrodite* who frequently groomed him. *Cruella* and *Pim* had been kept together before their addition to this group and retained their association.

Figure 3.12 illustrates proximity data for 16 subjects of Group 2 (although only 15 were kept together at one time). This figure illustrates that an increase in group size does not necessarily lead to an increase in proximity scores. An extra category has been added to this figure (> 7.5 %), because so few subjects were in proximity for more than 10 % of samples. The only 2 subjects who were in proximity on more than 30 % of samples were *Tolkien* and *Natasha*, who were kept together before their addition to this group. Other subjects who had previously lived together did not maintain their association, however. This was the first sub-group to be newly formed with subject pairs and trios from different caging areas who had not been in larger groups before. Other sub-groups illustrated (Figures 3.8 - 3.12) either previously existed or were added to. The members of this newly-formed sub-group were perhaps still adapting to the change in group structure, and were not spending as much time in proximity as members of sub-groups who had been together for longer.

Contact Data

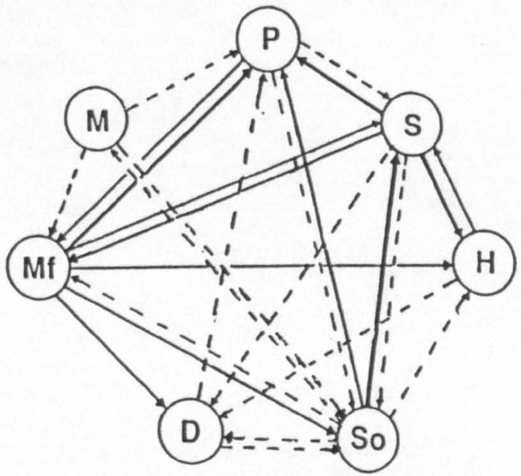
Subjects recorded in contact were usually playing together or grooming together, or occasionally resting in contact. Since most contact data involve grooming or playing, they will be covered in those sections below.

AFFILIATION

Social Grooming

Grooming relationships Subject Groups 1 a-c were the only sub-groups studied at the laboratory whose composition remained stable throughout their study period, therefore they are the only sub-groups whose grooming relationships shall be considered

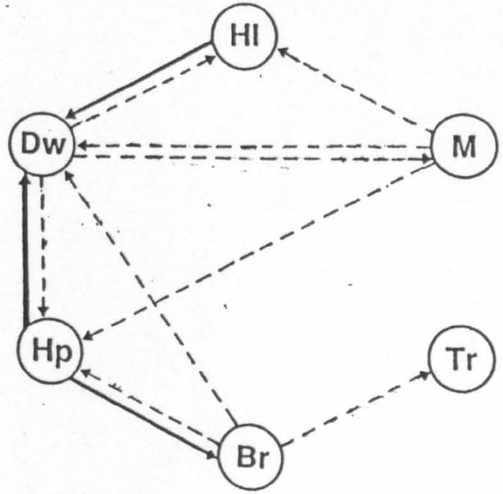
FIGURE 3.13 Grooming relationships, Group 1a.




* = not released

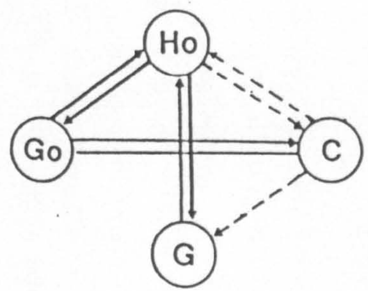
males : D - Daniel
So - Sokomodo
females : H - Hardtimes *
M - Maki
Mf - Miss Fields *
P - Putukin *
S - Samantha

FIGURE 3.14 Grooming relationships, Group 1b.




males : Br - Brutus
Hp - Hermaphrodite
Tr - Trokon
females : Dw - DmW
Hl - Helen
M - Maria

FIGURE 3.15 Grooming relationships, Group 1c.




* = not released

male : G - Ginger *
females : C - Carolla
Go - Goldilocks
Ho - Houdina

width of lines is proportional to % of samples the individuals were recorded grooming; arrows indicate direction of, grooming :

- - - 0.1 - 0.5
—— 0.6 - 1.0
—— 1.1 - 2.0
—— > 2.0

Note : in text (p.52), *inequality* in grooming refers to different categories for the amount of grooming given and received by the 2 subjects of a grooming pair (illustrated by different categories of lines connnecting the 2 subjects); *non-reciprocal* grooming refers to a one-way grooming interaction between 2 subjects (illustrated by a single line connecting 2 subjects).

here. Grooming relationships among these 3 sub-groups are illustrated in Figures 3.13 - 3.15. When these 3 figures are compared, there are differences between each sub-group, the main one being that in sub-groups 1a and 1b almost all possible grooming pair combinations occurred (85 % and 83 % respectively), whereas this was not the case for sub-group 1b (53 %). In most (75 %) grooming pairs for all 3 sub-groups, there was inequality in the amount of grooming given and received by each member of the grooming pair, and in 43 % of pairs grooming was not reciprocal. Generally, these differences are rank-related, with lower-ranking group members grooming higher-ranking group members more than they were groomed in return. Other factors may also influence grooming relationships, for instance the stage of a female's menstrual cycle may increase the amount of grooming she receives from males. This was particularly evident for *DmW* of subject group 1b (Figure 3.14). The adolescent male *Hermaphrodite* was recorded grooming her on 6 % of samples (which was the highest grooming score in any group). In the majority (67 % ) of samples when *Hermaphrodite* was recorded grooming *DmW* , she had a perineal swelling. This tendency for males to groom females more when they have an oestrous swelling was also found by MERRICK (1977) in a group of 6 captive chimpanzees.

<u>Grooming levels throughout the day</u> The grooming levels for subject groups 1a-c throughout the day are illustrated in Figure 3.16. These grooming levels can be related to the laboratory procedures, which are as follows.

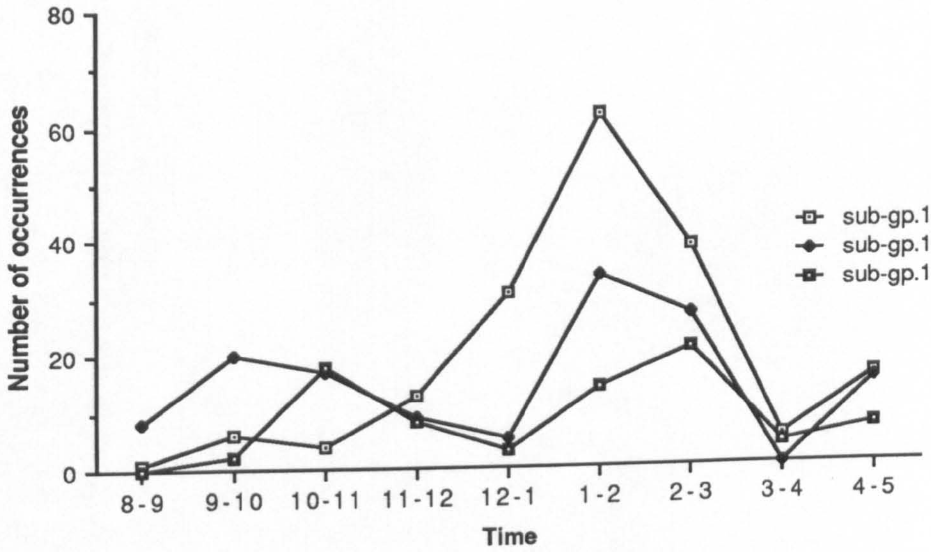
8.00 am - laboratory staff arrived. Any transfers between groups or removal of group members for experimental purposes (which was disruptive if it involved any group within sight) occurred between arrival and morning feeding.

9.30-10.30 am - morning feeding time (bread only). Chimpanzees did not get as excited by the morning feed as by the afternoon feed of fruit.

12.00-1.00 pm - laboratory staff on lunch break. Chimpanzees throughout the colony were generally more 'relaxed' during this time ( a subjective impression which is, however, supported by decreased levels of aggression at this time - see below) and they rested and groomed. Grooming levels reached a peak between this time and :

2.30-3.30 pm - afternoon feed, consisting of bread and fruit, which caused more excitement than the morning feed. Immediately before this feeding time, there was a marked increase in aggression (see below). The increased grooming levels may therefore indicate an increase in tension before the afternoon feed, with grooming serving to reduce tension between group members. Grooming as a tension reduction mechanism in

**FIGURE 3.16** Levels of social grooming throughout the day for Groups 1a-1c.

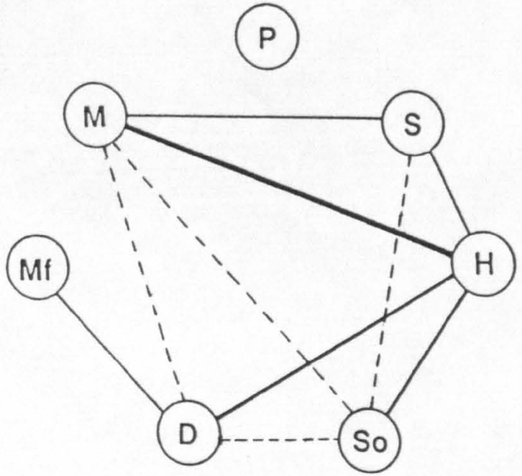



primates was discussed by TERRY (1970). De WAAL (1982:113, 1989a) also suggested that increased grooming between captive chimpanzees is a sign of friction.

There may, however, be 2 factors to take into consideration when considering grooming levels. Grooming may occur when tension within the group is building up, but also when the group is more relaxed, and grooming is not necessarily rank related. For example, after 4 pm, when the laboratory staff left, grooming levels rose again. The groups were relaxed during this period before going to sleep. The grooming level at this time does not rise to a comparable level to the early afternoon peak, which was probably more related to an increase in tension within the groups. WALLIS (1982) also found an increase in grooming before feeding time in captive chimpanzees, and also at the end of the day, before sleeping.

Social Play. Social play included both play-chasing and play- wrestling. Subjects involved showed a 'play face' (VAN HOOFF, 1967 b; GOODALL, 1968). Social play interactions for Groups 1a-1c are illustrated in Figures 3.17 - 3.19. The percentage of sampling intervals during which play was recorded ranges from 0 - 5 % in each sub-group, although the degree of involvement of each group member in these interactions varies between groups. In particular, *Brutus, Trokon, Hermaphrodite,* and *Helen* of Group 1b (Figure 3.18) took part in many play interactions. *Brutus*, the alpha

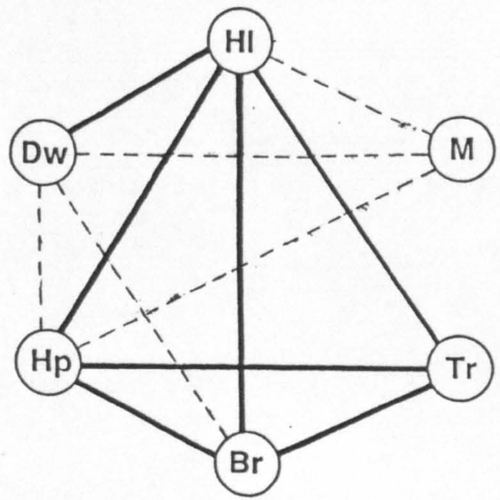
FIGURE 3.17 Social play interactions, Group 1a.




* = not released

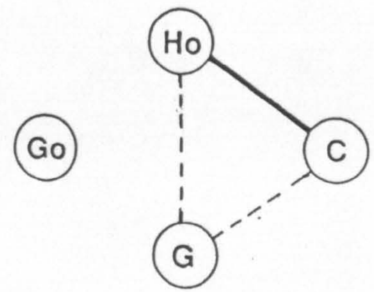
males : D - Daniel
So - Sokomodo
females : H - Hardtimes *
M - Maki
Mf - Miss Fields *
P - Putukin *
S - Samantha

FIGURE 3.18 Social play interactions, Group 1b.




males : Br - Brutus
Hp - Hermaphrodite
Tr - Trokon
females : Dw - DmW
Hl - Helen
M - Maria

FIGURE 3.19 Social play interactions, Group 1c.



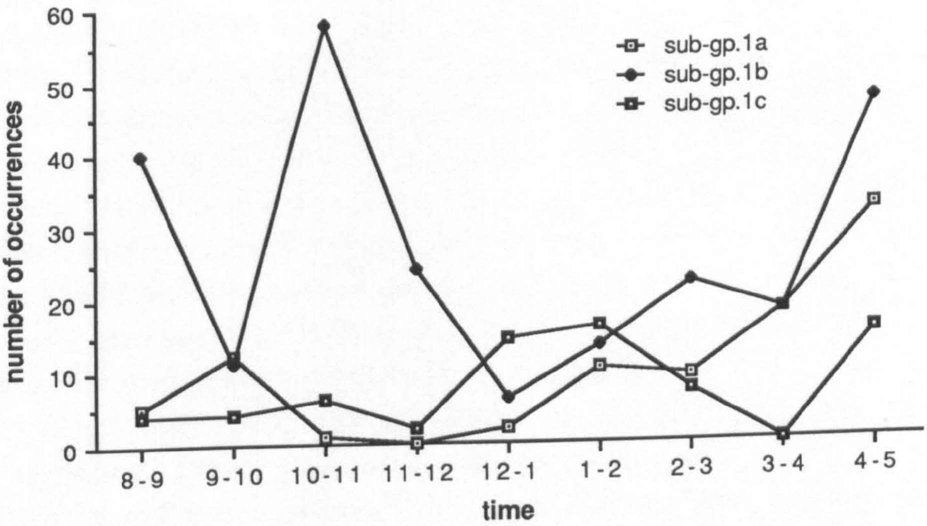

* = not released

male : G - Ginger *
females : C - Carolla
Go - Goldilocks
Ho - Houdina

width of lines is proportional to % of samples the individuals were recorded playing together :

- - - 0.1 - 0.5
— 0.6 - 1.0
— 1.1 - 2.0
— > 2.0

**FIGURE 3.20** Levels of social play throughout the day for Groups 1a-1c.




male of the group, was involved in more play interactions than the alpha males of sub-groups 1a and 1c. *Trokon* played more often than might be expected from his high solitary score, but play was one behaviour that distracted *Trokon* from his solitary stereotypies . Levels of social play throughout the day for subject groups 1a-1c are illustrated in Figure 3.20. The trend for higher levels of play in sub-group 1b could be related to the younger age of these group members, but levels of play are not significantly correlated with age (Kruskal-Wallis 1-Way Anova, $\chi2 = 4.27$, $p = 0.12$).

MERRICK (1977) reported that older group members played less than younger ones in a group of 6 captive chimpanzees, although the age range of the group varied only from 8-12 years. KING et al. (1980) reported that in a captive group of 7 chimpanzees, infants spent significantly more time playing than adults.

All groups also show a sharp increase in social play after 16.00 hours (Figure 3.20), when they were generally more relaxed.

## Sexual Behaviour

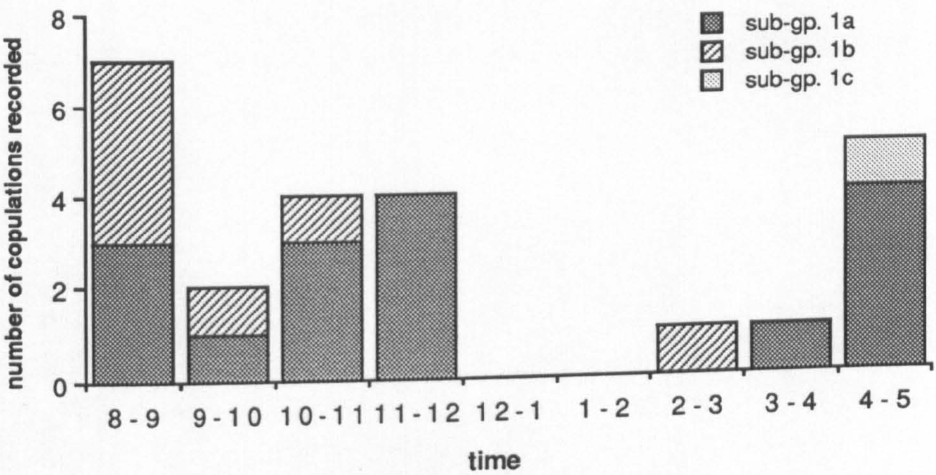
The chimpanzees showed the full range of normal sexual behaviour. Copulations involving adult females only occurred when the females had full perineal swellings, as occurs with wild chimpanzee populations (eg. TUTIN, 1980) and most captive populations (e.g. TUTIN & McGREW, 1973; WALLIS, 1982). In subgroup 1a, which contained 2 adult males, both *Daniel*, the alpha male, and *Sokomodo*, the second ranking male, copulated with females. *Sokomodo* on at least 2 copulations (of 6 observed) could be seen by *Daniel*. On 1 of these occasions *Sokomodo* moved out of *Daniel's* sight, attracted the female to follow him, then continued to copulate. On the other occasion where *Daniel* could see *Sokomodo* copulate with *Maki*, *Daniel* attacked *Maki* 4 minutes later. Similar situations have been observed in the Arnhem Zoo chimpanzee group, where the second and third ranking males of the group copulated, but usually did so when the alpha male could not see them (de WAAL, 1982 : 168 ).

Both *Daniel* and *Sokomodo* used idiosyncratic methods to attract females' attention for copulation. *Daniel* stood quadrupedally with his back to a wall, kicked one foot against the wall, then sat down with legs apart, displaying his erect penis. *Sokomodo* clapped his hands together when he sought to attract a female's attention for copulation. Wild male chimpanzees usually attract females by sitting with their legs apart, displaying their erect penis and looking directly at the female, although they have also been seen shaking branches and 'clipping' leaves before copulation (TUTIN & McGINNIS, 1981; NISHIDA, 1980).

*Brutus*, the alpha male of Group 1b was not seen to copulate with *DmW*, the only cycling female in his group. *Brutus* often inspected *DmW's* swelling and followed her around, but she seemed to be trying to avoid him whenever she had a swelling. She was seen to copulate with *Hermaphrodite*, an adolescent male of the group, and later with *Reagan*, another adolescent male who was added to the group before release.

*Ginger*, the adult male of Group 1c, was only observed copulating once with *Carolla*. *Goldilocks* was not cycling when she was in this group (although she developed a swelling almost immediately upon being transferred from this group, so she was probably reproductively suppressed while in *Ginger's* company due to his regular attacks on her). The other female of this sub-group, *Houdina*, showed regular swellings, and seemed 'bolder' while she had a swelling , by spending more time in proximity with *Ginger*, whereas at other times she avoided him and was often attacked by him. KOLLAR et al (1968) reported an increase in the dominance position of captive female chimpanzees while in oestrous. No copulations were observed between *Ginger* and

**FIGURE 3.21** Number of copulations recorded throughout the day for Groups 1a-1c.




*Houdina*, however.

The number of copulations recorded throughout the day for Groups 1 a-c are illustrated in Figure 3.21. There is a significant difference between number of copulations in the morning and afternoon (Binomial test, $p = 0.015$), although the total number of copulations (24) recorded throughout 56 hours of data collection is small. TUTIN & McGREW (1973) found a higher rate of copulations in the morning in a captive group of chimpanzees. For wild chimpanzees, GOODALL (1968 : 219) found that over two-thirds of copulations occurred in the mornings.

## AGGRESSION

### General levels of aggression

Aggressive attacks occurred most frequently upon addition of new group members, but also occurred in previously formed groups, usually immediately before and during feeding time. This is similar to the situation described by WILSON & WILSON (1968) in a group of 35-43 captive chimpanzees. Most large captive groups of chimpanzees are split up for feeding (see Table 2.1) to avoid the aggression which normally results from feeding large captive groups together.

Aggressive attacks by adult males in Group 1 were always preceded by an aggressive display. The males began by pant-hooting with pilo-erection, and ended their pant-hoot with a scream and charge around the enclosure, jumping on any chimpanzees who did not manage to avoid them. Occasionally they would grab and bite other group members, particularly *Ginger* of sub-group 1c, who often bit females of his group (see below). *Ginger* also added hand-clapping and wall slapping (while he walked bipedally) to his display. Adult males generally do not use their canine teeth when attacking females (eg. De WAAL, 1982: 104). *Daniel* (Group 1a) and *Brutus* (Group 1b) usually did not bite females at all, but slapped them on the back or jumped on their back. *Ginger* (Group 1c), however, frequently attacked and bit *Goldilocks*, and occasionally *Houdina*. Both females had many cuts and scars from previous attacks, sometimes deep cuts presumably from *Ginger's* canine teeth. *Ginger* was a male who had been kept as a pet until he was 7 years old, and so it is possible he had not learned appropriate limits for aggressive attacks. For this reason it was decided not to release *Ginger*, particularly since younger subjects were going to be added to the group. *Ginger* was later responsible for a serious attack on an adult female (who later died as a result of her wounds) and was thereafter caged alone.

Levels of aggression and 'disturbance' throughout the day for Group 1a - 1c are illustrated in Figure 3.22. Disturbance refers to any time the adult male of the group was displaying or any time the whole group was excited and vocalising (the latter situation occurring just before feeding time). Increased levels of aggression are correlated with increased levels of disturbance (Spearman's correlation, $r_s = 0.82$, $p < 0.05$). The two peaks in aggression occur at the morning and afternoon feeding times. When level of aggression is compared with levels of social grooming and social play (Figure 3.23), there are no significant correlations (Spearman's correlation, $r_s = 0.11, -0.08$, $p > 0.05$).

Aggression following transfers and additions

Attacks occurred most frequently after transfers between 2 groups or addition of new group members to a group. For Groups 1a-1c, the average number of aggressive encounters per hour varied from 0 to 4.7, depending on the time of day, whereas upon addition of new subjects to a group, the number of aggressive encounters increased to a rate of as much as 120 per hour. Usually the period in which aggression occurred lasted for 15-30 minutes following introduction, however in one extreme case when 2 groups were added together, aggressive attacks occurred for the following 5 hours, beginning with 100 attacks in the first hour and gradually decreasing. Some examples of introduction of new group members are discussed below.

1) *Addition of an (old) adolescent male to a group containing 2 adult males :*

In April 1985, before the release of the members of subject group 1, it was decided to introduce the 3 oldest males who would be released together. *Brutus*, who was in enclosure B (see Figure 2.6), was first transferred to the holding cage of enclosure A, where the 2 adult males, *Daniel* and *Sokomodo*, were housed. While *Brutus* was in the holding cage it was possible to watch *Daniel* and *Sokomodo's* reaction towards him while he was still separated from them by bars and was therefore protected from aggressive attacks. This was the case with all introductions, but it was felt to be particularly necessary on this occasion because introduction of males of this age had never been attempted at the laboratory before. Auditory contact and occasionally visual contact (see Figure 3.24) had been possible between these 2 enclosures, but there had never been any physical contact between *Brutus* and the other males before the introduction.

FIGURE 3.22 Levels of disturbance and aggression throughout the day for Groups 1a-1c.

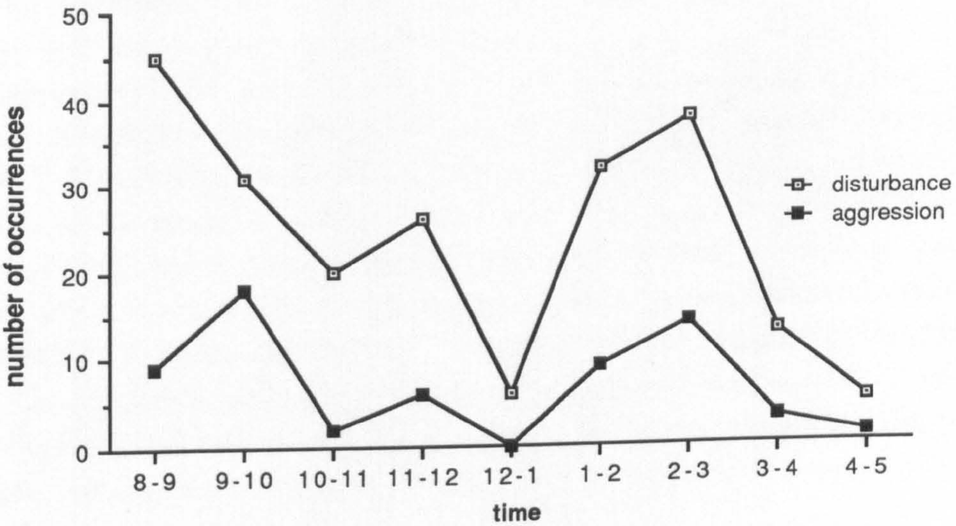
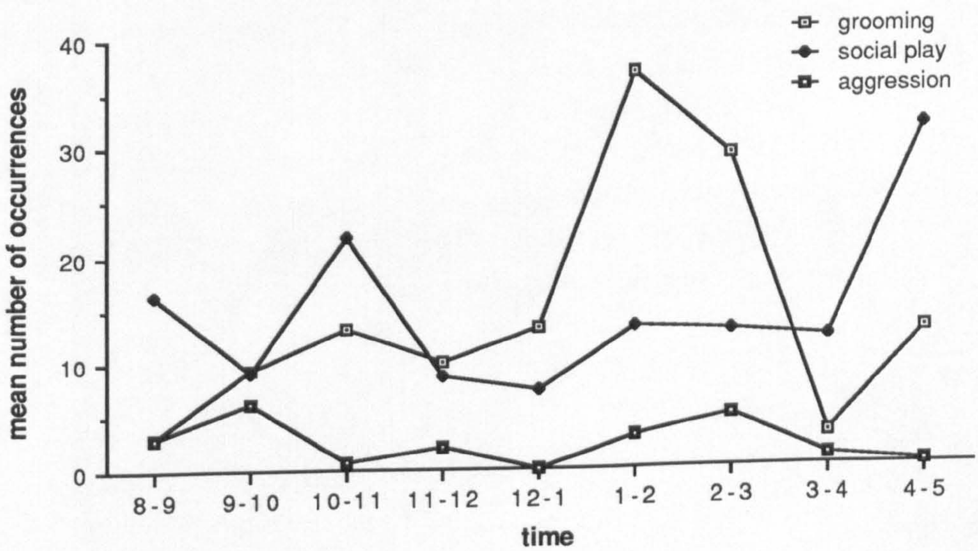



FIGURE 3.23 Levels of social grooming, social play, and aggression throughout the day for Groups 1a-1c.



When *Brutus* was first put into the holding cage of enclosure A, *Daniel* jumped onto the door of the cage and shook it vigorously. He was sprayed with a water hose to keep him back. *Sokomodo* also began to display, the first time he had been seen doing so during observations of this group. When *Brutus* approached the door of the cage, still not completely alert (because he had been given some anesthetic for the transfer), and held out his hand to *Sokomodo* (who could not be kept back with the hose), *Sokomodo* bit his thumb. The thumb was bleeding but did not require medical treatment. *Brutus's* reaction to the 2 displaying males was extremely submissive. He screamed almost continually and presented his rear to both males. *Daniel* was the first male to reassure Brutus, by touching him on the head and 'kissing' him. This occurred 45 minutes after the introduction. One hour after the introduction *Sokomodo* groomed *Brutus*. Immediately after *Sokomodo* had groomed *Brutus*, *Daniel* again began to display towards *Brutus*, who responded by bobbing submissively to *Daniel*, then grooming him. Ninety minutes after *Brutus's* addition to the holding cage of enclosure A, the group was calm again, but *Brutus* was kept in the holding cage overnight and let into the enclosure the following day.

When *Brutus* was let into enclosure A, there was little direct aggression between the 3 adult males. *Daniel* chased both *Sokomodo* and *Brutus* (5 and 4 times respectively in the first 25 minutes). *Daniel* attacked *Brutus* twice and *Sokomodo* once, but these attacks only involved slapping, with no biting. This was the first time *Daniel* was seen acting aggressively towards *Sokomodo*. *Daniel's* aggressive interactions towards both males seemed to occur after they had interacted. For example, when *Sokomodo* displayed in front of *Brutus* and *Brutus* responded by presenting submissively to him, *Daniel* then chased one or both of the males. For the first 17 minutes following *Brutus's* introduction to the enclosure, he spent most of the time on the climbing bar on top of the shelter, the highest point in the enclosure. He then came down from the bar and sat inside the shelter, in proximity with 3 adult females of the group. *Daniel* then entered the shelter and slapped *Brutus*, who ran out of the shelter screaming and climbed back onto the bar above the shelter. Thirty minutes after the introduction, all group members seemed fairly

**FIGURE 3.24** *Brutus* looking from enclosure B to enclosure A.

*Brutus* is standing on tyres balanced on top of the climbing frame in enclosure B, in an attempt to see chimpanzees in enclosure A. *DmW* is also standing upright behind *Brutus*. Chimpanzees in enclosure A could only be seen if they were standing on top of the climbing frame in enclosure A at the same time.

calm again. *Brutus* then groomed himself. Ninety minutes after *Brutus's* introduction the group was fed (with bread). *Daniel* displayed and ran around the enclosure. *Brutus* bobbed submissively to both *Daniel* and *Sokomodo* when they were eating their bread, and he sat next to *Sokomodo*. *Brutus* did not eat anything at this feeding time, but ate at the following feeding time.

The amount of aggression seen during this introduction was surprisingly low considering the aggressive interactions which can occur between strange males in wild chimpanzee communities (NISHIDA et al., 1985), although immature males may be able to transfer between different wild populations (TAKAHATA & TAKAHATA, 1989). Reports of introductions of adolescent and adult male chimpanzees in captivity have not been published. Perhaps such introductions are avoided because highly aggressive interactions are expected, but this introduction shows that it is possible. In fact, there was less aggression during this introduction than in the following introductions.

2) *Addition of 3 new females to a mixed-sex group* :

At the beginning of May 1985, *Carolla, Goldilocks* and *Houdina* were transferred from enclosure E to enclosure A, to be introduced to the other adult members of the group to be released. Fourteen aggressive attacks on these 3 females occurred within the first 27 minutes of introduction. The individuals attacking the new females were the adult males *Daniel* and *Sokomodo*, and the adult female *Hardtimes* . All 3 females were attacked. Thirty-one minutes after the introduction *Goldilocks* was seen bobbing submissively to the alpha male *Daniel*, and 41 minutes after introduction *Houdina* was seen bobbing to *Daniel*. No aggressive attacks were seen after the first 30 minutes, and the 3 females were successfully integrated into the group.

The above 2 examples were introductions where aggression occurred initially, but discontinued after a short time. However, not all introductions were achieved so easily. The following 2 examples describe introductions where further changes in group composition were necessary to achieve a stable group.

3) *Addition of some members of Group 2 to the younger members of Group 1* :

In February 1986 (laboratory study period 2, Figure 2.5), when the members of Group 1 were returned to the laboratory due to canal problems at the island, introduction of some new group members was attempted. The only previous attempts to add to an island group occurred in 1979, with the first island group released (Island D Group, Figure 2.4). These involved adding one or two individuals to an already established island group. These introductions were all unsuccessful, with the introduced individuals either being forced off the island, which resulted in drowning if they were not rescued in time, or else the individuals simply disappeared, presumably having been killed by the island group, or having been forced off the island when nobody was present to rescue them. The present study group, however, was the first group to be returned to the lab following release onto an island . There were individuals at the lab scheduled to be released, but no other islands available, therefore it was decided to attempt to add new individuals to the study group during their period at the lab. Another reason for the attempted additions was that the study group now only consisted of 12 individuals (see next chapter), and at this time there were still plans to attempt to release island groups into free-ranging sites. It was felt it would be beneficial to increase the group size to approximate more closely the size of communities of wild chimpanzees if release into free-ranging sites was a possibility.

On return to the laboratory, the members of Group 1 were split, with the older group members in one enclosure and the younger group members in the other. Six members of Group 2 (*Bill, Bertha, David, Natasha, Tolkien, Twebo*) were then introduced to the 5 younger members of Group 1 (*Blamah, Helen, Maria, Meryn, Popeye*). Although the new additions outnumbered the members of Group 1, they did not support one another in the way that the 5 members of Group 1 did, despite the fact that *Bill, Bertha, Natasha* and *Tolkien* had been living together before their introduction and were therefore familiar with one another.

With the exception of *Twebo*, all of the newly introduced group members were attacked by members of Group 1. Thirty attacks occurred within the first 15 minutes of introduction. Although attacks then discontinued, they occasionally resumed at feeding times, and sometimes at other times of the day throughout the next 2 weeks. Two weeks after this introduction, 4 females (*Anita, Mabel, Moffit, Tipsy*) were then also added to the group. This introduction was even more difficult than the previous one. The holding cage was opened for these new group members to go into the enclosure, but whenever they left the holding cage, *Maria, Helen,* and occasionally *David* continually attacked them until they returned to the holding cage again. Forty-five minutes after the holding cage door was opened, the new group members were still inside it. Occasionally *Helen* and *Maria* went inside the cage, in which case the new subjects had no way of avoiding attack. In an attempt to distract *Helen* and *Maria* from 'guarding' the holding cage door, a favourite treat for all group members (ice cream) was given out. While *Helen, Maria,* and other group members were eating ice cream, the 4 new group members entered the enclosure and the holding cage door was closed. *Maria* and *Helen* did not immediately resume attacking them when they were finished eating, but joint attacks by these 2 females on new group members occurred for the following 3 weeks, particularly at feeding times.

Since it was felt that the new group members were not obtaining enough food at feeding times, *Helen* and *Maria* were transferred from enclosure E to enclosure D, where the older members of Group 1 were housed. This did not solve the problem, however, because as soon as they were removed *David* and *Popeye* immediately took on the same role, and jointly attacked new group members. *David* in particular was very aggressive to other group members. In an attempt to solve this problem without further removals from the group, *David* and *Popeye* (sometimes with *Blamah* and *Meryn*) were separated into the holding cage at feeding times. At first this was easily done. They entered the holding cage when they were shown food, the door was locked and they were fed inside the cage while the others were fed in the enclosure. With time, however, it became increasingly difficult to separate *David* and *Popeye* into the holding cage. They entered cautiously and ran out as soon as the door began to drop.

Splitting the group at feeding time was therefore no longer a feasible solution to reducing aggression within the group, and 3 weeks after *Maria* and *Helen* were transferred to enclosure D, *David* was also transferred (where he was then the target of aggressive attacks by the adult females, the adult males having already been removed). This again failed to reduce aggression in enclosure E, since *Popeye* and *Blamah* were now the joint aggressors. For two weeks they were separated from the rest of the group at feeding times when possible, but when this became increasingly difficult to do, they were also transferred to enclosure D. The only member of Group 1 still in enclosure E with the new group members of Group 2 was the 6 year old male *Meryn* (Figure 2.9). Likewise *David* was the only member of Group 2 in enclosure D with members of Group 1. The members of Group 2a (see Table 2.3) were therefore not successfully introduced to members of Group 1 during their temporary (February - June 1986) return to the laboratory. For this reason, and also because there were no radio-collars available for members of Group 2a, they were not released when the members of Group 1 were returned to Island A in July 1986.

More group members (Groups 2b and 2c, Table 2.3) were added to Group 2a before some members of Group 1 were returned to the laboratory for a second time between December 1986 and May 1987 (laboratory study period 4, Figure 2.5). Since members of Group 2 had now been together longer and had formed a stable group, it was felt that a second attempt to introduce them to Group 1 might be more successful than the previous one. This introduction is described below.

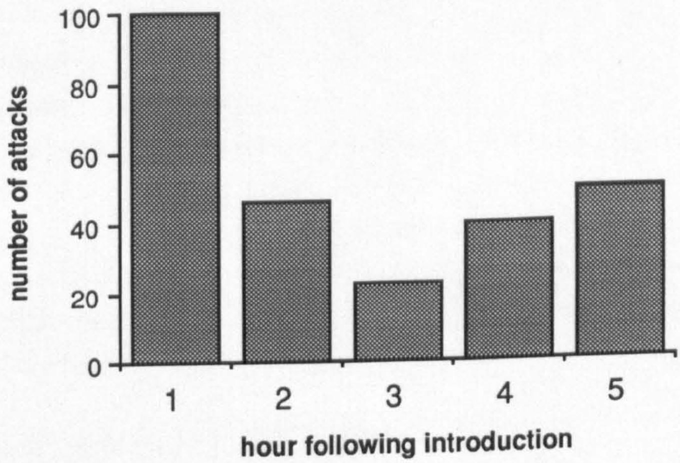
4) *Addition of all members of Group 2 to some members of Group 1* :

In May 1987, 25 chimpanzees housed in enclosures D & E (Figure 2.11) were

In May 1987, 25 chimpanzees housed in enclosures D & E (Figure 2.11) were mixed. Enclosure D contained a mixture of members of Groups 1 and 2, and enclosure E contained mainly members of Group 2. A door made of iron bars (1.5 x 2.0 m) had been inserted in the wall between enclosure D & E, allowing subjects from each enclosure to interact with one another. Subjects were seen grooming, copulating, and fighting through the bars of this door. Subjects had been able to interact in this way for 6 months before removal of the door, allowing subjects to pass freely from one enclosure to another. There had also been some transfers between the 2 enclosures during these 6 months.

The door separating enclosures D & E was removed in May, 1987, forming one group containing 25 subjects. This was the largest number of subjects which had been kept together at the laboratory. The addition of these 2 groups resulted in a great deal of aggression which continued for longer than that which occurred following the addition of some new subjects to groups, as described above. Aggressive attacks occurred within both enclosures, however, a second observer (Mary Richardson) was present, and recorded interactions within one enclosure while the author recorded interactions in the other enclosure. A total of 100 aggressive attacks were recorded in the first hour. This dropped to 23 in the third hour (Figure 3.25), but increased to 40 attacks in the fourth hour (which included feeding time).

**FIGURE 3.25** Aggressive attacks following introduction of two groups.



The adult females *DmW* and *Houdina* jointly attacked most of the subjects who had been in enclosure E, and they were responsible for 41.1 % of all attacks. *Blamah, Helen,* and *Maria* were responsible for a further 28.3 % of all attacks. The females of Group 1 therefore were the main aggressors, as had been found previously when attempting to add to their group. However, the members of Group 2 who had been kept together with these females in enclosure D were now also involved in aggressive attacks on other members of Group 2. In total, subjects from enclosure D were responsible for 94.2 % of all attacks which occurred. Of the small number of attacks by subjects from enclosure E (15), *Carolla* (Group 1) was responsible for 9 (60 %) of these. These were attempts to protect members of Group 2 when they were being attacked by *DmW* and *Houdina* of Group 1, but these attempts merely resulted in *DmW* and *Houdina* (sometimes together with *Helen* and *Maria*) redirecting their aggression towards *Carolla.*

Despite the number and persistency of attacks following this introduction, there were no serious injuries, and there were many affiliative interactions following aggression. Over the following 3 days, the 2 groups appeared to have 'swapped' enclosures, remaining in almost the same groups, but in the other enclosure. On the fourth day following introduction, 2 adolescent females from Group 2 (*Mabel & Twebo*), were separated into the holding cage of enclosure E because *DmW* and *Houdina* were still attacking them. They had some cuts on their ears and had not been able to get enough food at feeding times. They were held in the holding cage in contact with the other group members until they were transferred for island release 5 days later. The other 23 chimpanzees remained together in the 2 enclosures for 10-22 days, depending on which sub-group they were released in (see next chapter).

As an overall summary of these examples of aggression following introductions, generally it was found in most cases addition of new subjects to a group was possible, even addition of an old adolescent male to a group containing 2 adult males. Usually aggressive interactions occurred immediately following introduction, but soon discontinued. Most aggression occurred when 2 groups were mixed, and the attack frequencies per subject were much higher in this introduction. Joint attacks by 2 or more chimpanzees on new group members only occurred in groups with no adult males. Perhaps a dominance hierarchy is established more readily and with less aggression when a group contains a top-ranking alpha male.

## STEREOTYPED OR ABNORMAL BEHAVIOUR

Stereotyped behaviour in captive chimpanzees has been discussed by BERKSON et al (1963), DAVENPORT & MENZEL (1963) and DIENSKE & GRIFFIN (1978). WALSH et al (1982) use the term abnormal to describe behaviours that are species-atypical and occur exclusively or at much higher frequencies among animals reared in grossly restricted environments.The rearing conditions that tend to produce this state in captive chimpanzees include deprivation of maternal care, restrictive rearing, and nursery care by human caretakers.

DAVENPORT & ROGERS (1970) and MAPLE (1980) have described the resulting behavioural abnormalities produced by such restricted rearing. These include stereotypic behaviour, inability to initiate interactions with conspecifics, inability to respond appropriately to social overtures from conspecifics, reduced levels of play and social grooming, abnormal or absent sexual behaviour, abnormal and frequently abusive maternal care, and excessive dependence on humans.

Using WALSH et al. (1982) definition of abnormal behaviour, 11 of the 44 subjects involved in this study can be defined as showing abnormal behaviour. These 11 subjects are listed in Table 3.1, with some details of their rearing history and descriptions of their stereotyped or abnormal behaviours. Since WALSH et al. definition includes species-atypical behaviour, some behaviours which do not subjectively appear "disturbed" to human observers, but which are not in the normal behavioural repertoire of the chimpanzee (for example hand-clapping), are defined as abnormal.

Of the 11 study subjects who showed abnormal behaviour, only 9 were in the island release group. Of the 2 subjects not released, *Ginger* and *Putukin*, *Ginger* was not released because of his particularly aggressive behaviour, whereas *Putukin* was not released because her previous experimental history made her a suitable candidate for a further experimental protocol. All 11 subjects are included in Table 3.1, however, to show the full range of abnormal behaviour observed at the laboratory. WALSH et al. (1982) ethogram of 26 abnormal behaviours observed in a population of 91 chimpanzees (APPENDIX C) is used for the description of abnormal behaviours in this study, with the addition of descriptions of idiosyncratic abnormal behaviours shown by some subjects (Table 3.1).

When characteristics of these 11 subjects are compared with characteristics of the 33 subjects of the study group who did not show stereotyped behaviour (Table 3.2), there is a significant difference between the 2 groups in number of years kept as a pet. Details on the conditions in which subjects who were kept as pets were housed were not available, however. Pet chimpanzees could either be kept as part of a human family or housed alone in a cage (although presumably all pets spent some time alone in a cage). Pet chimpanzees reared in a human household would have more stimulation than those

**TABLE 3.1** Subjects (listed alphabetically) who showed stereotyped or abnormal behaviour. Subjects are

| Name | Sex | Age at capture (y) | Pet for (y) | No. of yrs. at lab. | Stereotyped/ abnormal behaviour |
|---|---|---|---|---|---|
| Bill | m | <0.5 | 1.5 | 5.0 | rocking (banging shoulder against wall) while self-clasping |
| Brutus | m | 1.0 | 3.0 | 4.5 | pulling hair (from his own fore-arms) |
| Carolla | f | 2.5 | 1.0 | 6.0 | sucks own big toe |
| DmW | f | 1.5 | 4.0 | 3.0 | head shaking (only when holding hand out for food) |
| Ginger display), | m | <1.0 | 7.0 | 3.5 | hand clapping and raspberry vocalisation (during aggressive<br>particularly aggressive behaviour |
| Goldilocks | f | 2.5 | 0.5 | 4.0 | head shaking with self-clasping (usually after aggressive attack) |
| Putukin | f | <1.0 | 0 | 8.5 | body rocking with self-clasping |
| Samantha | f | 1.0 | 0 | 8.5 | hair pulling (own and other subjects, including infants), mistreatment of infants (see HANNAH & BROTMAN, in press) |
| Sokomodo | m | 2.0 | >1.0 | 6.5 | raspberry vocalisation (only when grooming), hand clapping (when attracting females' attention for copulation) |
| Trokon | m | 0.5 | 3.0 | 5.0 | eye poking, body rocking (with self-clasping), squat walk *(a) pinch palm *(b) |
| Wolfram | m | 2.5 | 1.5 | 2.0 | presses tongue between lower and upper incisors and moves jaw continually up and down |

Stereotyped or abnormal behaviours are described in WALSH et al's (1982) ethogram (APPENDIX C)
Behaviours not included in this ethogram are described in table orbelow :

*(a) squat walk = sits with knees bent, legs in front of body, arms extended to side with hands on ground, then moves around by shuffling forward in sitting position

*(b) pinch palm = pinches palm of one hand with thumb and forefinger of other hand

**TABLE 3.2** Comparison of backgrounds of subjects who showed stereotyped behaviour with those who did not.

| | **Sex** | **Mean age at capture** | **Mean no. of yrs. as pet** | **Mean no. of yrs. at Vilab** |
|---|---|---|---|---|
| Subjects showing no ster./abnormal behr. (N=33) | 15m, 20f | 2.11 | 0.98 | 4.24 |
| Subjects showing ster./abnormal behr. (N=11) | 5m, 5f | 1.45 | 2.04 | 5.14 |
| Statistics | $\chi2$, $p>0.05$ | M-W, $z= -0.57$, $p=0.57$ | M-W, $z= -2.07$, **$p=0.04$** | M-W, $z= -1.2$, $p=0.23$ |
| | non-significant | non-significant | **significant** | non-significant |

M-W = Mann-Whitney U test.

kept alone for long periods in a cage, and would perhaps be less likely to show stereotyped behaviour. Such details were not available, however, therefore a finer comparison of rearing histories is not possible. The fact that those chimpanzees who were kept as pets for longer were more likely to develop stereotyped behaviour shows the detrimental effect this has on the development of normal behaviour.

A higher proportion of subjects who showed stereotyped behaviour belong to Group 1 (9 out of 26, 34.6 %) than to Group 2 (2 out of 19, 10.5 % ), which may be related to the fact that over a number of years Vilab chimpanzee housing changed from small indoor cages to larger outdoor cages, to outdoor enclosures. The members of Group 2, however, being younger, were not kept in the smaller indoor cages. Perhaps at least some of the stereotyped behaviour observed in members of Group 1 was due to being kept in less stimulating small indoor cages.

The subjects in the present study showed the full range of appropriate chimpanzee social behaviour, including social grooming, social play, aggression, and sexual behaviour. Even those subjects who showed stereotyped or abnormal behaviour were also involved in social interactions with other group members. The rearing history of individual chimpanzees may be a determining factor in their ability to adapt to a new environment. For example, the chimpanzees raised in restricted laboratory environments from PFEIFFER & KOEBNER's (1978) or CLARKE et al. (1982) studies seemed limited in their ability to adapt to a new environment in comparison to other studies involving chimpanzees who had been reared in better conditions and in groups (BREWER, 1982; GRZIMEK, 1970). The rearing histories of individuals in the present study group are more similar to those of the latter studies above, and they would therefore be expected to be good release candidates.

The collection of data on social behaviour before release in the present study allows a comparison of social behaviour before and after release, which will be discussed in chapter 7.

# CHAPTER 4

## BEHAVIOUR IMMEDIATELY FOLLOWING RELEASE

The aim of this chapter is to describe qualitatively the reactions of individual chimpanzees to being released onto a natural island after many years in captivity. Later chapters will report changes in behaviour following release, but to leave out their initial reactions would give the impression that adaptation to the new environment was as readily achieved by all subjects. This was not the case. Therefore, in order to avoid giving a false impression that every chimpanzee was automatically 'glad' to be set free from a cage, a few of the variety of reactions to release shall be described. It is difficult not to be subjective and anthropomorphic in giving such descriptions, but these seem worth including without systematic quantitative data to back them up, because to leave them out would give an incomplete picture of the release process.

### General release procedure

In transferring chimpanzees from the laboratory to the island, the following general procedure was used. Each subject to be transferred was anaesthetised with Ketaset (Ketamine Hydrochloride solution, 100 mg per ml, 2 - 4 ml., depending on weight). Ketaset was given by hand with a needle and syringe or by use of a blow-pipe and pressurised dart. Radio-collars were fitted if not already done so (Figure 4.1), and the chimpanzees were transported by boat to the island, a 45 - 60 minute journey. If the chimpanzees were in a small transporting cage or could be easily handled, they were allowed to recover during the journey, otherwise they were given a further injection of Ketaset to keep them anaesthetised for the entire journey.

On arrival at the island, usually between 11.00 and 13.00 hours, the chimpanzees were transferred into the cage (3x2x1 m) at the shore of the island (Figure 4.2). They were observed until fully recovered in case any fights began. On the occasions when fights did start inside the cage, the chimpanzees involved were splashed with water, which stopped them fighting. They were then kept in the cage overnight until 8.00 hours the next morning, so that a full day of observation would be possible on their first day of release. This allowed more time to look for chimpanzees if any went missing.

### Sub-groups for release

Subjects were split into sub-groups of 3 - 12 individuals for release, to allow closer

**FIGURE 4.1** Mary Richardson fitting a radio-transmitter collar.

FIGURE 4.2 Holding cage at shore of Island A.

Top - Saffa looking into holding cage
Bottom - Sokomodo dispalying on top of holding cage

monitoring of subjects, and to allow younger and lower-ranking group members to become familiar with their new environment before release of higher-ranking group members. It was felt that this would make the initial adaptation to the island less stressful for lower-ranking group members. For the initial release of Groups 1 and 2, the sub-groups for release are listed in Tables 4.1 and 4.2.

### Group 1

Release of sub-group 1

The first sub-group released was the largest one. In retrospect, it was too large (for reasons given later). Surprisingly, there were no fights between the 12 subjects as they recovered from anesthesia in the cage at the shore of the island. Instead, they seemed to be more concerned with looking at their new surroundings. The chimpanzees seemed to be subdued, but all accepted their usual food of fruit and bread which they were given inside the cage.

The following morning at 8.00 hours, the chimpanzees were set free after fruit and bread had been put around the shore in the expectation that some subjects might need some encouragement to leave the cage. As soon as the cage door was opened, however, all 12 subjects immediately rushed out and within one minute were all out of sight. .Three males, however (*Franco, Meryn, Trokon*), apparently did not run too far away and returned to the feeding area within a few minutes. On this day, there were more people on the island than at any other time, since Betsy Brotman and Alfred Prince of the New York Blood Centre had come to watch the release. Together with John Zeonyuway, Joseph Thomas, and Jessie Smythe (3 of the laboratory staff), this gave a total of 6 people, which was perhaps an intimidating sight for the chimpanzees.

The 6 humans began to walk around the island in search of the other 9 chimpanzees, followed closely by the 3 males who had returned to join us. These 3 made a mixed group : *Trokon* , who exuberantly ran backwards and forwards along paths, was extremely confident and almost immediately seemed to have a changed personality compared with when he was at the laboratory and showing solitary stereotyped behaviour. *Franco* seemed to have problems walking on uneven surfaces and frequently stumbled on roots, etc. *Franco* had suffered from some sort of neurophysiological problem early in life, but this had not been a problem when he was at the laboratory and was walking on flat surfaces in cages and enclosures. *Meryn* wanted to be carried, and repeatedly tried to climb up onto peoples' backs. When he was not allowed to do so, he had temper tantrums, and screamed and rolled on the ground slapping himself. A

**Table 4.1** Sub-groups for release,Group 1.
Subjects are listed alphabetically within sub-groups.

| **sub-group & release date** | **subject** | **radio-collared** | |
|---|---|---|---|
| 1. 7/6/85 | Blamah | x | |
| | Cruella | x | |
| | Franco | | + |
| | Helen | x | |
| | Hermaphrodite | | + |
| | Knut | | + |
| | Maria | | + |
| | Meryn | | + |
| | Pim | x | |
| | Popeye | x | |
| | Reagan | x | |
| | Trokon | | + |
| 2. 22/6/85 | Carolla | x | + |
| | DmW | x | + |
| | Goldilocks | x | |
| | Houdina | | + |
| 3. 20/7/85 | Grace | | + |
| | Maki | x | |
| | Samantha | | + |
| | DmW (2nd time) | | + |
| 4. 13/8/85 | Brutus | x | |
| | Daniel | x | |
| | Sokomodo | x | |

+ = wearing radio-collar
x = not wearing radio-collar
x + = not wearing radio-collar on release, but later had one fitted

**Table 4.2** Sub-groups for release, Groups 1 & 2.

| sub-group & release date | subject | radio-collared |
|---|---|---|
| 1. 3/6/87 | Blamah (SG1) | x |
| | Maria (SG1) | x |
| | Meryn (SG1) | x |
| | Big Sore | + |
| | Mabel | + |
| | Saffa | + |
| | Telle | + |
| | Wolfram | + |
| 2. 8/6/87 | Bahnti | + |
| | Bertha | + |
| | Bill | + |
| | Dr. Me | + |
| | Moffit | + |
| | Tipsy | + |
| | Tolkein | + |
| | Twebo | + |
| 3. 11/6/87 | Carolla (SG1) | x |
| | Helen (SG1) | x |
| | Anita | + |
| | Jimbo | + |
| | Mango | + |
| | Natasha | + |
| 4. 16/6/87 | Goldilocks (SG1; E) | x |
| | Popeye (SG1; E) | x |
| 5. 17/6/87 | Houdina (SG1) | x |
| | DmW (*SG1) | + |
| | David | + |
| 6. 22/6/87 | Samantha (SG1; E) | x |
| | Sokomodo (SG1; E) | x |
| 7. 2/7/87 | Brutus (SG1; E) | x |
| | Grace (SG1; E) | x |

+ = wearing radio-collar, x = not wearing radio-collar
SG1 = subject Group 1, others are from subject Group 2
SG1; E = member of Group 1 who had been on Island E for the past 6 months
*SG1 - DmW was originally a member of Group 1, but was returned to the laboratory shortly after release . She then remained there until the release of Group 2 in 1987,when she was successfully released.

compromise was reached, and I walked holding *Meryn's* hand as he walked tripedally next to me.

About an hour later, *Popeye, Blamah,* and *Hermaphrodite* joined us. *Hermaphrodite* seemed to be torn between wanting to avoid people, but also wanting to stay with the other 5 chimpanzees who were now following us. He followed at a distance, occasionally whimpering when he was out of sight until he had caught up again. We continued to look for, and call the others, then decided to split up into 2 groups.

At 12.00 hours, 4 hours after release, when the author and Betsy Brotman were sitting at the feeding area, *Maria, Helen,* and *Knut* approached. This was the first time they had been seen since release. Perhaps they had been avoiding the larger group of 6 people, but were less intimidated by 2 people.

By then, the only 3 subjects who had not been seen were *Cruella, Pim,* and *Reagan.* In fact they were never seen again, despite many searches on Island A and B in the following weeks. *Cruella* and *Pim* were assumed to be travelling together, because they had been kept together at the laboratory, and had retained their association when they were added to the larger group. Presumably they were avoiding people, because they must have seen or heard people looking for them. It was not known if *Reagan* was with them or alone.

At the end of this first day on the island, the group of 9 chimpanzees who had joined us were fed. Three, *Maria, Helen,* and *Knut,* then left the feeding area when it was becoming dark at 18.30 hours. *Helen* seemed reluctant to follow *Maria,* and whenever *Maria* got too far ahead, *Helen* began to whimper. In response, *Maria* returned, put her arm across *Helen's* back, and they walked together. This was an example of how companions could help one another in adjusting to their new environment.

The other 6 chimpanzees remained at the feeding area. The cage at the shore of the island was left open in case any of the chimpanzees wanted to sleep inside it. When we left the island, *Trokon, Meryn,* and *Popeye* were inside the cage, *Hermaphrodite* and *Blamah* were sitting in a tree, and *Franco* was sitting on the ground. *Meryn* began to whimper as the boat left the island, apparently unhappy to be without human companions. *Meryn* continued to do this for a week after release, sometimes actually having tantrums when we left the island in the evenings.

Over the following days, *Franco* continually became lost, and was unable to keep up with the others. It was therefore decided he should be returned to the laboratory. He was easily coaxed into the cage at the feeding area, given an injection of Ketaset by hand, and transferred to the boat for return to the laboratory.

Release of sub-group 2

The 4 females of sub-group 2 were released onto the island without any problems. The 7 chimpanzees already on the island were at the feeding area when these 4 were released. These 11 had not all shared the same enclosure at the laboratory, but there was no aggression when they were released. This time, the subjects to be released were fed before release, so that if they avoided people to begin with, at least they had been given some food first. These 4, however, immediately joined the others, and did not rush off as soon as they were released. On walking around the island, 3 of the 4 newly-released females followed the others, but *Carolla* seemed to become lost and sat in a tree screaming until the author (followed by *Meryn*) returned for her, and led her back to the rest of the group. *Goldilocks* seemed much more confident on the island than at the laboratory, where she had been a target of aggression. *Carolla* and *DmW* travelled alone a lot in the next few days, and had to be found before feeding times. *Houdina* seemed to adjust well and travelled with the others.

A few days after *DmW's* release, she had a respiratory infection and seemed very lethargic. She was therefore returned to the laboratory. She actually seemed glad to be back at the laboratory, was much more alert, and seemed so enthusiastic to return to a cage that she was not tranquillised before opening the transporting cage. The door of the transporting cage was opened and she walked right into a laboratory cage.

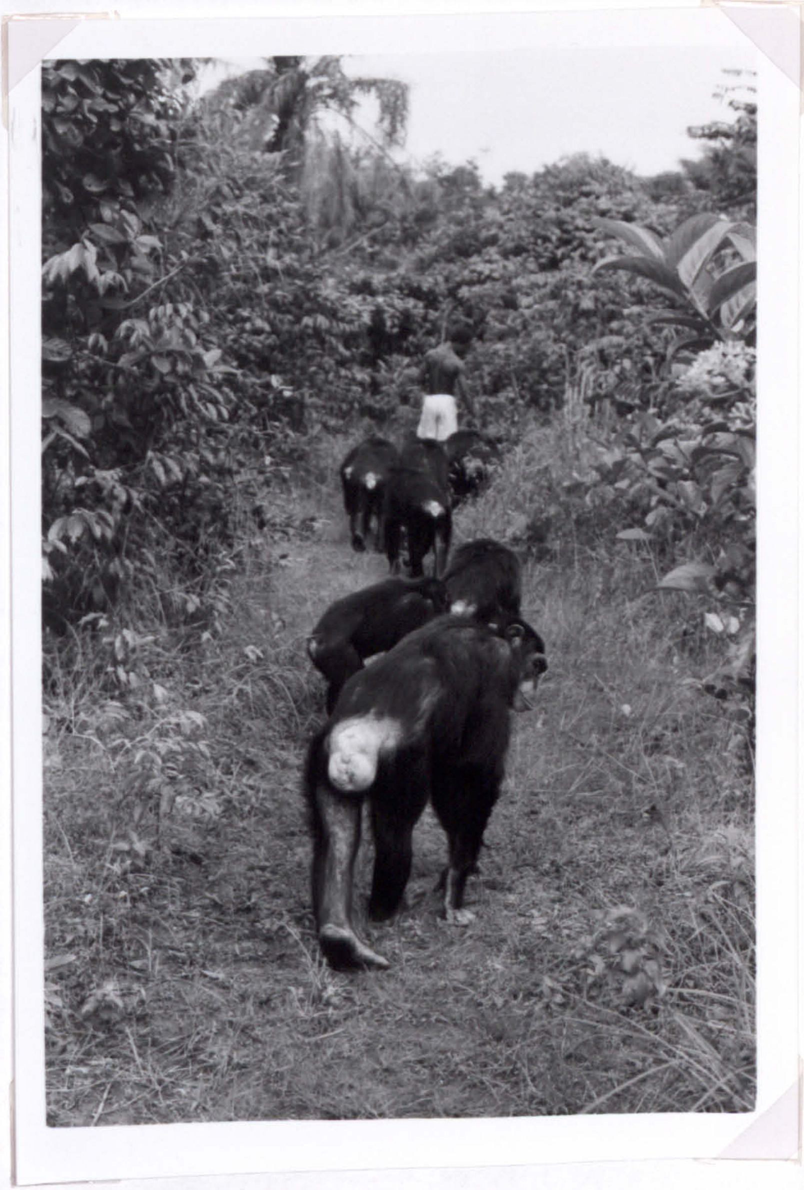
Six days after her release, *Carolla* still had to be found every day at feeding time. She also still occasionally sat in trees screaming until she was found. She was now wearing a radio-collar, however, and so she could be found more easily.

At this stage most of the group on the island developed respiratory infections. They were given medication daily in milk or Kool-aid (a sweet-flavoured drink) if they did not drink milk. Meanwhile no further sub-groups were added.

Release of sub-group 3

On 20 July 1985, another 3 females, *Samantha, Maki,* and *Grace* were released. The tide was high when the cage was opened, which meant the chimpanzees had to step into water in order to get onto the island. *Samantha*, however, immediately jumped onto a branch of a nearby tree from the top of the cage. The other 2 females remained inside the cage for the following hour. It was decided that if humans moved away from the feeding area, which usually resulted in the chimpanzees following (Figure 4.3), this might encourage them to leave the cage and follow. When the human observers and most of the

**FIGURE 4.3** John Zeonyuway walking on Island A, followed by chimpanzees.



group of chimpanzees were in the interior of the island almost one hour later, *Grace* and *Maki* approached with *Hermaphrodite* (who was following these 2 females who had sexual swellings). There had been some doubt about whether *Grace* would be too old to adapt to release. She appeared to have no problems, however, and was also one of the most vigilant group members, often standing upright to look ahead if she thought she heard something, or giving a 'woo' alarm call and rushing into a tree, with the others responding by also climbing into trees. *Grace* appeared to be settling into the cage to sleep on her first night on the island when the author was leaving at 18.30 hours. *DmW* was also inside the cage with her.

Release of sub-group 4

The 3 oldest males of the group, *Daniel, Sokomodo*, and *Brutus*, were the last to be released onto the island. They were kept in the cage at the island overnight for release them the next day, but on the day they were due to be released, *Samantha* did not come to the feeding area. She was found, using the telemetry equipment, with a new-born baby. Since we were not sure if it would be possible to walk around the island following the release of the older males, it was decided to keep them in the cage for longer until we were sure *Samantha* and her baby were alright. For the following 4 days, *Samantha* avoided the rest of the group, and did not come to the feeding area. She was found each day and was given some food wherever she was found. On the 5th day following the birth of her baby, *Samantha* arrived at the feeding area with her new baby, accompanied by *Grace*.

Now that *Samantha* was travelling with others again and coming to the feeding area, it was felt *Daniel, Sokomodo*, and *Brutus* could soon be released from the cage on the island. On arriving the following day, however, we found the cage empty. The 3 males had pulled up some of the floorboards of the cage and escaped through the hole they had made.

*Daniel* and *Sokomodo* soon arrived at the feeding area, displaying, but calmed down when they were given some fruit. *Brutus* was not with them and he was missing for the following 6 days, despite searches for him on Island A and B. On the seventh day, *Brutus* was seen in the mangrove area between Island A and B, when we were returning by boat from Island B, following a search there for him. *Brutus* was at the edge of the river and although he moved back a little when the boat approached, he then returned when the boat motor was turned off and we stepped ashore. We attempted to coax *Brutus* onto the boat to return him to Island A, because it would be very difficult for people to walk from there to Island A to lead him back. He approached the boat, but would not get into it. We had no Ketaset to anaesthetise him, so we then went slowly in the boat, stopping occasionally next to the mangroves and calling *Brutus*, in an attempt to lead him in the direction of Island A. This did not work, however, so we decided to return for him the following day. He seemed to have been in the same area for the past few days, because there were 3 fresh nests in the tall mangroves close to the river, and no other chimpanzees had been in this area. *Brutus* was found in the same area the next day, was anaesthetised, and returned to Island A. He did not go missing again, and travelled with the others.

Removals, illness, and death

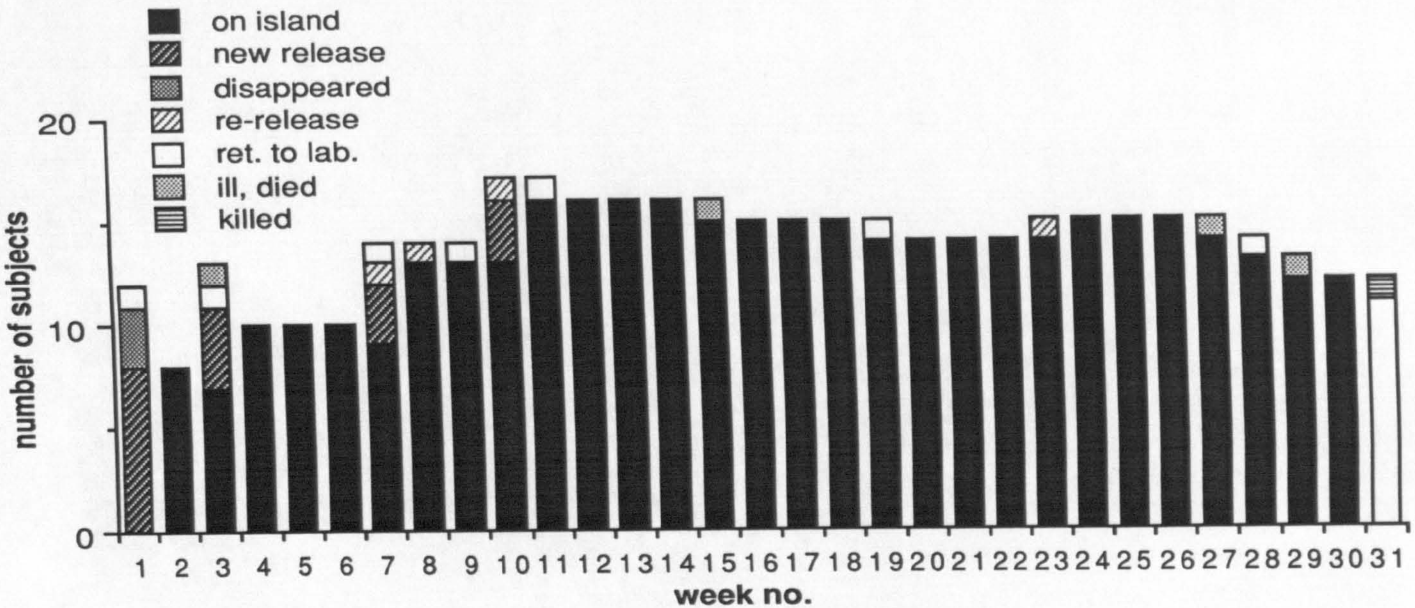
During the 7 months following release, some subjects were removed from the island because they did not adapt, some because they were ill, or some disappeared immediately following release and were not seen again. If subjects were returned to the laboratory because they were ill, and they then recovered, they were re-released. Over the 7 months, the release group dropped in size from 22 to 12 subjects (11 on the island and 1 on a temporary return to the laboratory). The changes in group composition during this time are summarised in Figure 4.4. It can be seen from Figure 4.4 that even subjects who had gone through an initial period of adaptation to the island became ill and died as much as 30 weeks after release.

In January 1986, 31 weeks after release, the adolescent male *Hermaphrodite* crossed the canal separating Islands A and B from Island C (Figure 2.4). He was found dead on Island C, with numerous wounds, apparently having been attacked and killed by the chimpanzees on Island C. To prevent further aggression between the 2 groups, the study group was transferred from Island A to the laboratory until the canal was made deeper by further digging to prevent chimpanzees from crossing.

Re-release of Group 1

In June 1986 (i.e. island study period 2, Figure 2.5), the 12 remaining members of Group 1 were re-released onto Island A. There were obvious differences in the subjects' reactions to their second release, compared with their first release. They were not unsure and nervous as before, but instead were extremely excited when they were let out of the cage and embraced one another. They walked around the island and ate natural foods more confidently than they had done on their first release. They all knew their way

**Figure 4.4** Changes in composition of Group 1 following release.




**Legends :**

on island = subject on island for 1 week or more
new release = subject released onto island for first time
disappeared = subject not seen following release
re-release = subject re-released onto island after a temporary return to the laboratory
ret. to lab. = subject returned to the laboratory (ill or not adapting)
ill, died = subject who was ill and later died (sometimes following return to the laboratory)
killed = subject who was killed by chimpanzees on adjacent island (after crossing the canal)

around the island, and there were no losses. Subjects also came to the feeding area when the boat arrived and did not have to be found as had been the case for some subjects on their first release.

In November 1986, the subjects on Island A were again transferred to allow re-digging of the canal separating Islands A and B from Island C. Half of the group was transferred to Island E (Figure 2.4), and the other half was returned to the laboratory.

Release of Groups 1 and 2

In June 1987, Groups 1 and 2 were released onto Island A (see Table 4.2). For this release, 16 radio-collars were available, therefore all 17 subjects of Group 2 were radio-collared for release (with one collar being transferred from a member of the first sub-group released to a member of the third sub-group released). As well as this difference from the initial release of Group 1, the members of Group 2 also had 'role models' to learn from, because they were being released together with members of Group 1, who already had experience of living on Island A.

In terms of individual responses to release, however, there were still a few members of Group 2 who did not seem to adapt as readily as the others. For example, *Twebo* at the beginning often sought out human company, and tried to 'tandem-walk' with people by walking bipedally behind someone, putting an arm around each of this person's legs. Sometimes, she also split away from the group and became lost. She may have been avoiding the group because she was occasionally the target of aggression of females of Group 1 (which she sometimes responded to by climbing onto a human). *Twebo* wore a radio-collar, however, and was found and led back to the rest of the group.

*Saffa* also left the group and was found using the telemetry equipment. *Saffa* was the first subject to be radio-tracked who tried to avoid being found. He continually moved away each time the author (followed by the other chimpanzees) got close to him. Had he not been wearing a radio-collar at this time, he would not have been found. *Saffa* was a low-ranking group member, and was occasionally a target of aggression of members of Group 1. When this occurred he either fled, or ran toward people. He was therefore assumed to be avoiding the other chimpanzees rather than people on the occasions when he was trying to hide. *Saffa* was the only member of Group 2 to become ill after release. He was returned to the laboratory one week after release because he was very weak and lethargic and had lost weight. He was re-released on Island A one week later.

Other subjects who tried to avoid being found while being radio-tracked were

*Natasha* and *Anita*. In their case, however, they seemed to be avoiding people rather than other group members. They soon became accustomed to coming to the feeding area, however, and accepting food given to them by humans.

In the same way as *Maria* and *Helen* of Group 1 seemed to support one another following their first release, *Moffit* and *Telle* of Group 2 also had a close association which probably helped them during their initial adjustment to a new environment. They were often observed tandem-walking during their first week on the island but rarely thereafter. For some subjects at least, the presence of a companion probably made the release process less stressful.

One male of Group 2, *Jimbo*, was returned to the laboratory almost immediately after his release because he was found to be extremely unpredictable and aggressive towards people. His aggression was unusual because it did not follow the usual male pattern of some sign of impending aggression before an attack, with clear signals such as displaying and piloerection. Instead, *Jimbo* appeared friendly towards humans until he was close enough to either grab or bite them. *Jimbo* had shown this type of behaviour at the laboratory, but it was hoped that he would not be as aggressive towards humans following release. However, he was. To keep *Jimbo* on the island would have meant more restricted access for humans, and since the follow-up of released subjects was important, it was decided to return him to the laboratory. *Jimbo* had been kept as a pet for 6 years and had only recently been resocialised in order to be released. In contrast to his interactions with humans, *Jimbo* was very submissive and low-ranking among other chimpanzees.

During the 2 months the author was present following the release of members of Group 2, all subjects (with the exception of *Jimbo*) remained on the island. In the following months, however, in the author's absence, an adolescent male from Group 2, *Tolkien*, was found drowned, presumably from having been forced off the island in an aggressive encounter. A second male, *Wolfram*, was later found dead with many wounds. Following this incident there were various removals from the island group to try to solve the problem of aggression. There were no further deaths. Despite the fact that in the end some members of Group 2 had to be returned to the laboratory following aggressive attacks by members of Group 1, this release can still be considered the most successful in the sense that there were no disappearances and no deaths from illness. Differences in long-term success rate between various releases will be discussed more fully in chapter 8.

**FIGURE 4.5** John Zeonyuway and Alex Mulbah at rest area on Island A with chimpanzees.

Interactions with humans

In general, the chimpanzees interactions with humans were affiliative. For example, chimpanzees sometimes groomed or attempted to play with human observers. It was possible to follow the chimpanzees closely and sit amongst them (Figure 4.5). Chimpanzees were interested in any objects (such as a camera or the telemetry equipment) taken onto the island by humans, and attempted to touch them, but did not forcibly try to take them unless they were put down.

On some occasions, chimpanzees were aggressive towards people. The alpha male *Daniel* sometimes displayed and charged towards people during the first weeks of release, but thereafter accepted people walking around the island. The chimpanzees still acted aggressively towards any strangers who attempted to go onto the island, however.

The above examples were just a few illustrations of some subjects' initial behaviour following release. There were differences in initial reactions to release, but following this first period of adjustment, most, if not all subjects were then capable of learning a variety of behavioural patterns which illustrated their adaptation to their new circumstances. These will be discussed in the following chapter.

# CHAPTER 5

## SUBSISTENCE BEHAVIOUR AND DAILY LIFE AFTER RELEASE

### FORAGING AND DIET

#### Choosing which foods to eat

For the first few weeks following release, the chimpanzees on Island A were offered the same amount of food that they were given at the laboratory, with bread in the morning and fruit in the afternoon. Therefore, they were not forced to forage for wild foods which occurred on the island. Soon after release, however, the chimpanzees began to eat foods such as leaves and small fruits. Their intake of wild foods gradually increased until they were not able to eat the same quantity of provisioned food, with some food being left uneaten. Provisioning was then gradually decreased (see below).

In the wild, infant chimpanzees learn which foods to eat through observation of their mothers, and by first tasting pieces of food being eaten by their mothers (e.g., GOODALL, 1968; 193, 237). In some cases, mothers have also been observed preventing infants from eating unsuitable foods (HIRAIWA-HASEGAWA, pers. comm.). But what of chimpanzees released into a natural environment after many years in captivity ? All subjects in this study were wild-born and therefore may have retained some memory of eating wild foods. Although it would be unlikely that they would remember which foods would be suitable to eat, even if they did occur on the island, at least the fact that they had once had experience of eating wild foods may have meant that they accepted such foods more readily than captive-born chimpanzees would have done. In their chimpanzee rehabilitation projects, BREWER (1982) and CARTER (1981) found that captive-born chimpanzees were more reluctant to eat wild foods than were wild-born chimpanzees.

#### First release of Group 1

The time it took for members of Group 1 to accept wild foods is illustrated in Figure 5.1. It can be seen from this figure that members of the first sub-group released were more reluctant to eat wild foods than were members of subsequently released sub-groups. For the first sub-group, who had no role models to observe, some hesitation in eating unknown wild foods would seem to be a sensible strategy. The only 2 males of sub-group 1 who ate wild foods on the first day were the two males *Franco* and *Trokon*.

These two males gave the impression of not being particularly selective in what they were eating, picking and eating leaves in an apparently random fashion. *Franco* was returned to the laboratory 5 days after release because he was not physically capable of travelling with the others (as described in the previous chapter). *Trokon* was on the island for longer, however, he also was returned to the laboratory 3 weeks after release because he was ill. He had bacterial diarrhoea (*Shigella* sp.) which was treated, but he did not recover fully and died after return to the laboratory. *Trokon* had continued to be less discriminating than the others in what he was eating. Even when the others were regularly eating specific parts of particular species he ate any parts. For example, *Trokon*, on seeing a small group of chimpanzees eating the seeds from the middle of the flowers of *Heisteria parviflora*, rushed up and grabbed a whole branch, then ate all the leaves from the branch he had picked. Although these leaves are not known to contain any toxins (HARRISON, pers. comm.), it is possible that *Trokon* was eating other unsuitable foods during his 3 weeks on the island which had harmful effects.

In the 2 weeks members of sub-group 1 were on the island before the release of other sub-groups, they had developed choices of particular species of leaves and they ate all small fruits, both ripe and unripe (see Figure 5.2). When the next 3 sub-groups were released, they observed the others eating and then ate the same species themselves. The fact that they saw other chimpanzees eating these species seemed to be enough encouragement for them to eat the same things, often on their first or second day on the island. Usually subjects only ate small numbers of leaves or fruits on their first day on the island, then gradually increased their intake.

There was a delay in observing members of sub-group 4 (the 3 oldest males) eating wild foods because during the first few weeks following their release, little time was spent on observations in the interior of the island, where most foraging occurred. In the first week following release of the three older males, searches were carried out for *Brutus*, who had gone missing. During these searches, although the chimpanzees usually followed the people walking around the island, there were no stops by humans at the chimpanzees' favourite feeding areas. After *Brutus* was found, observations were restricted to around the feeding area. For the next 2 weeks, the author and John Zeonyuway or Joseph Thomas only took very short walks along paths leading from the feeding area, until all people involved felt confident about spending time in the interior of the island without fear of aggression from the older males. On the first day that observations of the 3 oldest males were carried out in the interior of the island, all 3 were observed eating fruits and leaves. This was almost one month after their release. It seems likely, however, that they had been eating wild foods much earlier than this, particularly

*Brutus* who was missing for his first week on the island. *Brutus* did not get any provisioned food during the first week when he was missing, but was healthy and in good condition when he was found.

Second release of Group 1

When the members of Group 1 were released for the second time, they began eating wild foods within minutes of release, without the hesitation they had shown on their first release. They made 'food grunts' when they arrived at fruiting trees and all ate fruits. In fact they did not eat very much provisioned food during their first days on the island, in contrast to when they were first released in 1985, when they relied mainly on provisioned food. On the first day of this second release, at least one female, *Blamah*, had eaten indigestible leaves, because they were seen opportunistically the following day in her faeces. Following this, undigested leaves were not seen again in her faeces.

Release of Group 2

When the members of Group 2 were released onto Island A in June 1987, they were released together with members of Group 1 who had experience of living on Island A, and could therefore serve as role models. The first sub-group was released together with *Blamah*, *Maria*, and *Meryn* of Group 1. When there were no people on the island, the members of Groups 1 and 2 apparently did not travel together, because they arrived separately at the feeding area each day. When people were present, however, all of the chimpanzees travelled together with the people, which meant that at these times the members of Group 2 had the opportunity to observe *Blamah*, *Maria*, and *Meryn* of Group 1 eating wild foods. Comparing the first sub-groups for release in Groups 1 and 2 (Figures 5.1 and 5.3), the first members of subject group 2 released accepted wild foods more readily (60 % of first sub-group on day 1) than the first members of Group 1 (22 % of first sub-group on day 1)who were released without role models to observe. This difference is not statistically significant, however (Fishers exact probability test, $p = 0.27$). The member of Group 2 who was most reluctant to eat wild foods was *Saffa*, who avoided all other group members during his first weeks on the island, and therefore had less opportunity for observing and learning from the others.

FIGURE 5.1 Acceptance of wild foods following release, Group 1.

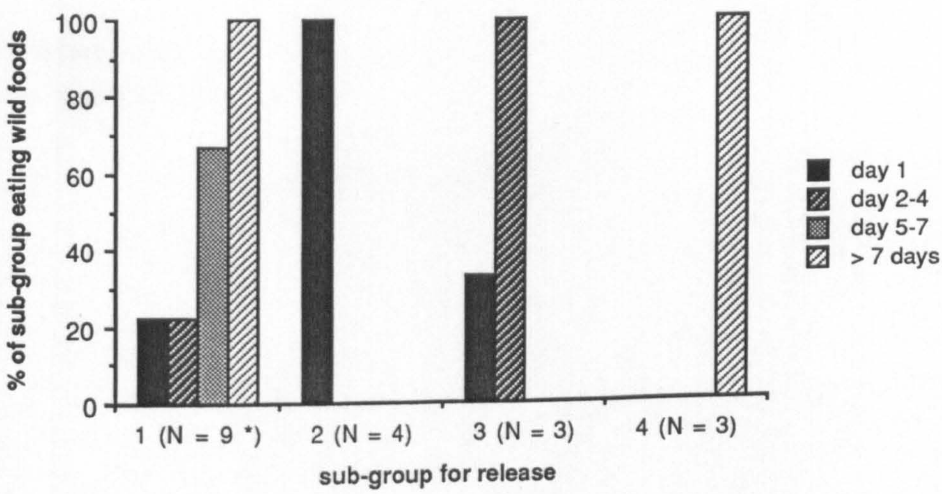
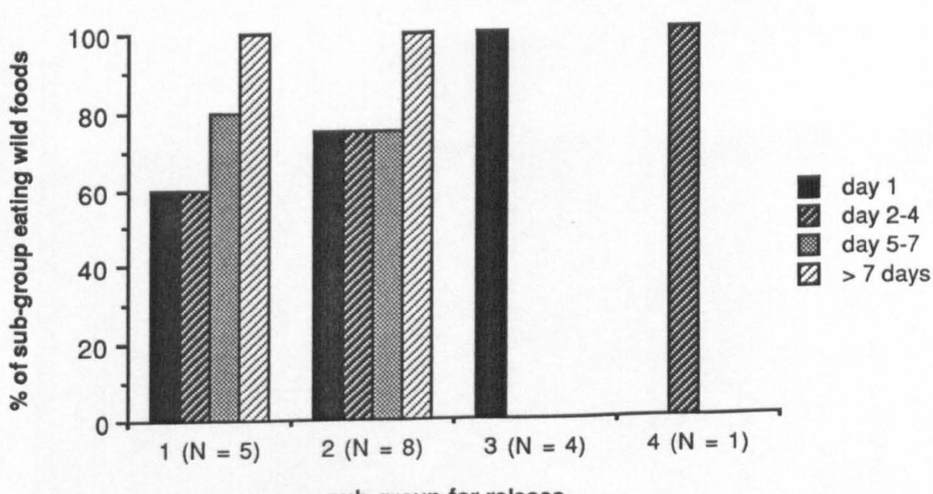



FIGURE 5.3 Acceptance of wild foods following release, Group 2.




These figures illustrate the first time subjects from each sub-group were seen eating wild foods, beginning with the day they were released (day 1). * Subjects who disappeared immediately upon release, or who were returned to the lab. immediately after release, are not included in these figures. Members of Group 2 were released with members of Group 1.

**FIGURE 5.2**

Chimpanzees eating naturally occurring foods on Island A.

Decrease in provisioning

Following the release of all sub-groups onto Island A, provisioning was decreased to once per day instead of two times per day, and over the following months was gradually decreased from 7 days per week to 3 days per week, and occasionally 2 days per week at times of the year when the chimpanzees were finding more foods to eat on the island. There was not enough variety and quantity of foods available on the island for the chimpanzees to become totally self-sufficient, however, although small groups of 2 or 3 individuals could find enough food to support themselves for 1 - 2 weeks. For example, in October 1985, one female (*Goldilocks*) and 2 adolescent males (*Hermaphrodite* and *Knut*) did not come to the feeding site for 13 days (*Knut* returned after 10 days). When a search was carried out for them, they were found on Island B (having crossed the mangrove area between Islands A and B - see Figure 2.4). When they were found, all 3 were in a fruiting *Parinari excelsa* tree, and had handfuls of *Parinari* fruits, which they were eating. They did not seem particularly hungry, but accepted fruit which had been brought for them. This appeared to be a 'consort trio' (see next chapter). Thereafter, when *Goldilocks* had a swelling and travelled either with both males or with *Hermaphrodite* only, they were not searched for and returned to Island A for provisioning when Goldilocks' swelling had passed its stage of maximal tumescence.

ANT-EATING

Observations of wild chimpanzees using tools to obtain social insects have been reported from various sites across Africa, covering the ranges of all 3 sub-species : *Pan t. verus* , BALDWIN (1979), McGREW (1983b), BOESCH & BOESCH (1989); *Pan t. troglodytes*, JONES & SABATER PI (1969), SUGIYAMA (1985); *Pan t. schweinfurthii*, McGREW (1974), NISHIDA (1973).

Only one possibly inhabited termite mound (*Macrotermes* sp.) was found on Island A, with a few other very old remains of termite mounds. No termite activity was seen in this mound during the study period, and the island chimpanzees never showed any interest in it. Chimpanzees released onto an island in Gabon (HLADIK, 1973) also ignored *Macrotermes* spp., which were abundant, although they used tools to obtain ants and ate several species of termites.

The chimpanzees in the present study did, however, begin to eat weaver ants

(*Oecophylla longinoda*), which are the most commonly eaten species across the various populations of chimpanzees (GOODALL, 1968; McGREW, 1983b). Weaver ants construct arboreal nests from living leaves which they bind together with larval silk. Each nest contains about 5g of eggs, larvae, and adult forms (HLADIK, 1973). The nests can be conveniently plucked from trees by hand, and therefore can be obtained without tool-use .

The first subject seen eating weaver ants was the adolescent female *Popeye*. Six weeks after release, *Popeye* was seen jumping out of a tree with a weaver ant nest in her hand. She first ate the ants which were rushing out of the nest onto her hand, by picking them from her hand with her lips, then she systematically peeled off leaves, eating the ants and ant larvae inside and discarding the leaves. *Popeye* did not first crush the nest, which would have stopped the ants streaming out of the nest in defence, a technique employed by wild populations of chimpanzees (GOODALL, 1986 : 231; BALDWIN, 1979). *Popeye*, by jumping out of the tree, had avoided the ants on the branches surrounding the nest, which bite in defence of their nest. On another occasion, however, *Popeye* was seen to jump out of a tree covered in weaver ants, roll on the ground, then pick ants from her arms and back.

Within the same week when Popeye was first seen eating weaver ants, 2 other subjects were seen eating weaver ants using the same technique as *Popeye*. Three weeks after *Popeye* was first seen eating eating weaver ants, the 3 older males of Group 1 were released, after which few observations were carried out in the interior of the island for the following month. When observations were resumed in the interior of the island, 4 other subjects were seen eating weaver ants, 1 using the same technique as *Popeye*, and 3 using a different technique. These 3 ate ants without picking the nest, by grasping a branch which had a nest on it, pulling the branch towards them, then with their lips picking off ants as they rushed along the branch in defence and onto their hand. These 3 chimpanzees were always on the ground when eating ants in this way, and were therefore restricted to eating ants within their reach since they did not climb into trees to obtain ants from higher nests. They also did not eat any ant larvae, since they did not open any nests.

The 7 subjects who were seen eating weaver ants are listed in TABLE 5.1. Observations of ant-eating were rare (only 16 observations during 2 months of observations in the interior of the island). It is possible that other subjects may have eaten weaver ants at other times, but were not seen doing so.

**TABLE 5.1** Eating of weaver ants (*Oecophylla longinoda*).

| Name | Sex | Date 1st seen eating ants | Method used |
|---|---|---|---|
| Blamah | f | 19/9/85 | [1] |
| Brutus | m | 22/9/85 | [2] |
| Helen | f | 21/7/85 | [2] |
| Hermaphrodite | m | 24/7/85 | [2] |
| Maria | f | 19/9/85 | [1] |
| Popeye | f | 20/7/85 | [2] |
| Samantha | f | 19/9/85 | [1] |

Subjects are listed alphabetically.

**Method :**

[1] = pulls down branch and eats ants walking onto hand.

[2] = picks nest and eats ants, larvae, and pupae inside

## NEST-BUILDING

### Introduction

In the wild, chimpanzees construct nests in trees for sleeping in each night. Early reports of nest-building by wild chimpanzees are summarised by YERKES & YERKES (1929), and later by IZAWA & ITANI (1966). Infant chimpanzees for the first 3 or 4 years of life, sleep with their mothers at night and have no need to construct their own nests (GOODALL, 1962,1968). Infants and juveniles therefore have many opportunities to observe their mothers building nests, and they also frequently construct small nests during the day, often as a form of play (GOODALL, 1968 : 200). Young chimpanzees therefore have up to 5 years of practice in nest-building before they have to build their own nests for sleeping in.

BERNSTEIN (1962), in a study of nest-building abilities of wild-born and captive-born laboratory chimpanzees, found that all 7 wild-born subjects built a nest of some form, whereas of the 18 captive-born subjects, 3 built good nests, 5 built crude nests, and 10 never built nests of any sort. Of the 3 captive-born subjects who built good nests, 2 had previously participated in studies of nest-building (in groups where they may have had the opportunity to watch others building nests), and 1 had been raised by her wild-born mother for the first year of life. Some previous experience, either in the form of the opportunity to watch others or to manipulate branches and twigs, therefore seems to be necessary for the development of nest-building behaviour.

In the present study, in order to test their nest-building abilities before release, the members of Group 1 (a-c) were given piles of cut branches in their laboratory enclosures. Their nest-building abilities at the laboratory could then, in some cases, be compared with their nest-building behaviour on the island.

### Nest-building Before Release

In April 1985, 2 months before their release, the members of Group 1 (a-c) were given cut-branches in their laboratory enclosures and their reactions observed for the following hour. Between 7 and 10 branches were provided per subject. Branches were up to 2 m long and had many side branches. When the branches were dropped into the enclosures from above, there was an initial period of excitement lasting for a few minutes, then most group members took some branches. They were first seen tasting leaves from the branches or stripping bark from the branches, then they began to build nests. In some cases, access to branches was rank-related (see below), and lower-ranking group members obtained fewer branches with which to build nests. All subjects, however, made some attempt to build nests, and were given a nest-building score. The nest-building score was a cumulative score from points for different components of nest-building behaviour shown, such as gathering branches, bending branches together, and attempting to make a nest above ground-level. Nest-building scores are listed in Table 5.2. Scores vary from 1 to the maximum of 7.

In general, better nests were built by higher-ranking group members because they had access to more branches. For example, the oldest males of each sub-group (*Daniel, Sokomodo, Brutus, Ginger*) were the ones who first took large piles of branches for themselves, and they could leave their 'nest' and collect more without fear of other subjects stealing the branches they already had. Several branches had been provided for each subject to build a nest, but higher ranking group members took lots of branches and built one very large nest or 2 or 3 nests, abandoning one and beginning another in a different location . All of the older males made circular piles of intertwined branches, with a depression in the centre in which they sat. *Ginger* soon lost interest in his nest, however, and only then did the 2 of the 3 females of his group begin to make nests. The third female, *Goldilocks*, was interested in the branches, and approached and looked closely at *Ginger's* abandoned nest, but *Ginger* chased her from it. Thereafter, *Goldilocks* sat in a corner rocking, a stereotyped behaviour she showed at stressful times when *Ginger* was likely to become aggressive, such as feeding times. *Goldilocks* did not touch any branches, although she was seen gathering sand around herself when she was sitting in the a corner. Her low nest-building score was therefore more likely to be a result of her fear of taking any branches rather than a lack of interest or ability.

Another subject limited by his inability to obtain branches was *Trokon* of sub-group 1b. *Trokon* showed interest in the branches, but whenever he tried to collect some, he was chased by the alpha male of the group, *Brutus*. On two occasions when he had managed to get one branch, the branch was taken from him by *Hermaphrodite* then *Helen*, and they each added the branch to the nests they were building. On another occasion, *Trokon* attempted to take a branch from an abandoned nest of *Hermaphrodite's*, but *DmW*, who was using these branches to make a new nest, would not let him take any. *Trokon* then went to a corner with 5 small pieces of twig (20 - 30 cm in length) which he had picked up around the enclosure. He carefully arranged these twigs in a circle around himself in the sand and then lay down inside the circle. This recalls KOHLER'S (1927) findings that when insufficient material was provided to captive chimpanzees, they arranged it in a circle around their bodies, but did not form a supportive structure.

The third subject with a low nest-building score, *Maki* of Group 1a, had access to branches, but did not show any manipulation of branches, although she did sit in nests made by other subjects.

Most nests were built on the sand floors of the enclosures (Figure 5.4), always against a wall (Table 5.3), as was also found by BERNSTEIN (1962). Four subjects, however, did carry branches on top of the shelter and 3 built nests there.

Subjects moved around a lot from one nest to another (Table 5.3), either by dragging branches from an already constructed nest, then rebuilding it in another location, abandoning the nest altogether and starting a new nest with new branches, or taking over a nest abandoned by another subject and sometimes continuing to work on it.

The chimpanzees, although they showed some appropriate components of nest-building behaviour, did not seem to regard their nests as sleeping structures, even though branches had been supplied at 17.00 hours, when they normally began to settle down for the evening. When the branches had lost their novelty, and it was beginning to get dark (one hour after the branches were put into the enclosures), the chimpanzees went inside the shelter or lay on the sand as they normally did in the evening. Perhaps the closest approximation the subjects could get to sleeping in a nest at the laboratory when no materials were provided was to balance a tyre on top of the climbing bar (the highest structure in the enclosure), and rest inside it.

### Nest-building after release

#### Sleeping in trees and nest-building

Following release, it was difficult to determine the sleeping habits of each subject for a number of reasons. First, the subjects had a habit of remaining at the feeding area if there were still people on the island, some because they seemed to want to stay in human company, others perhaps because they were waiting to see if they would be given more food. Therefore, remaining on the island until dusk sometimes only resulted in the chimpanzees still sitting around in the feeding area. When sub-groups were seen to leave the feeding area in the evenings, it was not always possible to follow them in the dark, particularly because they sometimes travelled through the tall mangroves at the edge of the river, a popular location for nests. Walking on the island after dark was also more

**TABLE 5.2** Nest-building scores at the laboratory for members of subject group 1 (a-c).

| Name | Shows interest in branches | Gathers branches together | Forms circle around body with branches | Bends branches together | Carries branches on top of shelter | Makes nest on top of shelter | Uses nest for sitting/ resting in | Score |
|---|---|---|---|---|---|---|---|---|
| a) Daniel | + | + | + | + | + | | + | 6 |
| Maki | + | | | | | | + | 2 |
| Samantha | + | + | + | | | | + | 4 |
| Sokomodo | + | + | + | + | | | + | 5 |
| b) Brutus | + | + | + | + | + | | + | 6 |
| DmW | + | + | + | + | + | + | + | 7 |
| Helen | + | + | + | + | + | + | + | 7 |
| Hermaphrodite | + | + | + | + | | | + | 5 |
| Maria | + | + | + | + | | + | + | 6 |
| Trokon | + | | + | | | | | |
| c) Carolla | + | + | + | + | | | + | 5 |
| Ginger * | + | + | + | + | | | | 4 |
| Goldilocks | + | | | | | | | 1 |
| Houdina | + | + | + | + | | | | 4 |

Subjects are listed alphabetically within sub-groups

* not released, but is included in table because he influenced the others' behaviour

**TABLE 5.3** Nest-building behaviour at laboratory, subject group 1 (a-c).

| | Name | Nest-building score | *(Built nests on island)* | Nest location | No. of times nest was moved | Comments |
|---|---|---|---|---|---|---|
| a) | Daniel | 6 | ? | on ground, against walls | 5 | had more branches than females |
| | Maki | 2 | ? | inside shelter | 0 | sat in others nests, but did not manipulate branches |
| | Samantha | 4 | + | inside shelter; against front wall | 4 | |
| | Sokomodo | 5 | ? | on ground, against walls | 5 | had more branches than females |
| b) | Brutus | 6 | + | on ground, against walls | 11 | moved nest a lot, sometimes building new one right next to previous one |
| | DmW | 7 | ? | on top of shelter; against shelter; inside shelter | 2 | made nest on top of shelter |
| | Helen | 7 | + | on top of shelter; inside shelter | 3 | made nest on top of shelter |
| | Hermaphrodite | 5 | + | against shelter | 3 | |
| | Maria | 6 | + | on top of shelter; inside shelter | 3 | most times used others nests, but made one nest herself |
| | Trokon | 2 | ? | on ground, in corner | 1 | could not get enough branches to make substantial nest |
| c) | Carolla | 5 | +(*G) | inside shelter | 0 | only one of group who used nest to rest in |
| | Ginger * | 4 | - | inside shelter; in corner | 1 | initially interested, but soon lost interest in branches |
| | Goldilocks | 1 | ? | none built | 0 | looked at Ginger's nest, but was too afraid to touch branches, sat rocking |
| | Houdina | 4 | + | inside shelter; on ground against wall | 2 | |

* - Ginger was not released, but is included because he influenced the others' behaviour

*G - only seen building ground-nests on the island

All data is from the laboratory, apart from the inclusion of observation of nest-building on island for easy comparison with lab. nest-building score.

**FIGURE 5.4** Nest-building at Laboratory.

likely to result in aggression towards people by the alpha male of the group (ZEONYUWAY, pers. comm.).

Once, however, when some subjects left the feeding area in the evening and did not travel too far to be followed, they were seen to lie on tree branches and not in nests. The three females who were seen resting on branches, *Maria, Helen*, and *Goldilocks*, had all been on the island for one month at this point, and had apparently not begun to build nests. Two weeks later, however, *Helen* was seen building a nest, and *Maria* was seen lying in one (which was not freshly-built). Following this, 2 new nests were seen 3 times in areas where *Maria* and *Helen* were known to have travelled to on the previous evening.

The first time *Houdina* was seen building a nest, she used an unusual technique of breaking a branch from one tree, then climbing into another tree with it and making her nest there. In the wild, chimpanzees normally use materials within reach of the site they have chosen to build their nest, and they have been reported (GOODALL, 1968 : 199) to abandon their nest and start again in another place if there are not enough branches available. *Houdina* had built her nest in a tree at the feeding site, and the trees in this area were almost bare because they were used so much by the chimpanzees while they were at the feeding site. Houdina had chosen a supporting fork in a tree which did not have many other branches around it, but had taken a branch with her with which she made her nest in the tree fork. She was not seen doing this again.

Sleeping on ground/in feeding cage

One evening, while trying to see if subjects were building nests in trees, I found*Maki* lying on the ground. She seemed quite settled, with her head resting on an arm and her eyes closed, and it was already beginning to get dark, so I assumed that this was where she had planned to sleep for the night. This was 4 days after *Maki's* release, and during this time she had not been seen climbing trees like the others. Ten days after *Maki's* release, however, *Maki* was seen climbing in trees, and although she was once seen falling from a tree and into the edge of the river because she had climbed onto a brittle branch, her climbing skills seemed to improve. It was not clear if she had also begun to sleep in trees during her 2 months on the island before she was returned to the laboratory because she was ill.

Some subjects made use of the cage at the feeding site during their first nights on the island. Two subjects, *Meryn* and *Blamah*, were thought to be sleeping on top of the cage during their first nights on the island. *Meryn* always remained at the feeding site as long as there were people there, and even when the others began to leave when they could see that people were leaving the island, *Meryn* remained, watching the boat depart. *Blamah*, who had lived with *Meryn* for a number of years at the laboratory, seemed to wait for him. One night when they were both last seen sitting on top of the cage, there were 2 crude nests on top of the cage the following morning, and so it was assumed that they had probably made them.

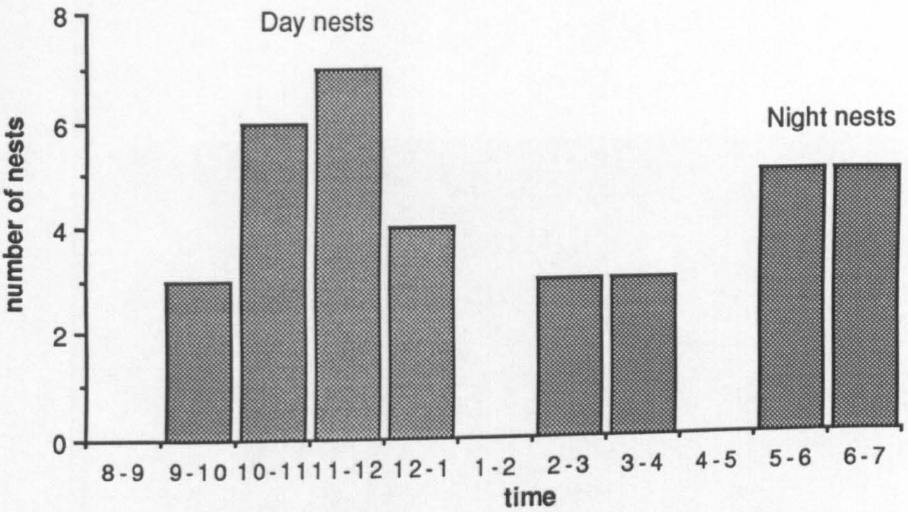
One female, *Grace*, was twice seen during her first week on the island taking branches inside the cage, and making a nest there. Another female, DmW, was also inside the cage with Grace on these evenings, and may also have been sleeping inside the cage. Following the first week of release, however, there were no more signs of chimpanzees sleeping inside or on top of the cage, and the subjects who had done so were assumed to be sleeping in trees like the others.

<u>Day nests</u>

Construction of nests for resting in during the day has been reported for several populations of wild chimpanzees (REYNOLDS & REYNOLDS, 1965b; IZAWA & ITANI, 1966; GOODALL, 1968; JONES & SABATER PI, 1972). In these different populations, day nests were made both in trees and on the ground.

On the island, the study subjects were also seen building day nests, both on the ground (62 %), and in trees (39 %). Day nests were built until 16.00 hours (Figure 5.6), whereas night nests were built from 17.30 hours onwards. Only nests which were seen being built are included in Figure 5.5. There is a slight peak in number of nests built from 10.00 - 12.00 hours, which is a little earlier than the rest period the chimpanzees tended to show at the laboratory from 12.00 - 13.00 hours, when laboratory staff were gone for lunch. This supports the explanation that the rest period at the laboratory was related to the absence of staff and any laboratory procedures. However, another possibility is that at the laboratory, where there was less access to shade, the chimpanzees were resting at the hottest time of day. On the island, however, where the chimpanzees could be continually in the shade (unless they chose to sit in the clearing at the feeding area), they were perhaps less influenced by temperature peaks in direct sunlight.

**FIGURE 5.5** Time of nest-building on Island A.




Ground nests

*Carolla* of Group 1 was seen building 7 day nests on the ground, but was not seen building nests in trees. The members of Group 2 began building ground nests immediately after release, but were not seen building nests in trees. They were only observed for 6 weeks following release, however, and since chance observations of building night nests in trees were rare with Group 1, and were only recorded more than one month after release, it is felt that the absence of observations of members of Group 2 building nests in trees is due to lack of data rather than any lack in their ability.

*Carolla*, the member of Group 1 who built ground nests, but not nests in trees, did not seem to regard her nests as sleeping or resting structures. For example, one morning while walking around the island, *Carolla* broke a branch from a tree, made a crude ground nest on the path, and sat in it (Figure 5.6). When the others had all walked past her, she then left her nest and caught up with with the rest of the group. *Carolla* made 4 of these nests on paths between 10.00 and 10.30 hours on this occasion, although at other times (3), she was seen making only 1 nest. These other nests were also on paths and were also only used for a few minutes. Other subjects made day ground nests at the feeding area, or at a small clearing (from previous cultivation) in the interior of the island where the chimpanzees often rested. As well as building day nests for resting in, subjects

**FIGURE 5.6** Carolla in crude ground nest on Island A.

often lay on the ground to rest during the day. There were no predators on Island A, therefore it was safe for chimpanzees to rest on the ground.

Nest-building abilities before and after release

Due to the lack of island nest-building data for members of Group 2, only members of Group 1 will be included in a comparison of nest-building abilities before and after release.

Comparing nest-building scores at the laboratory (Table 5.3) with observations of nest-building on the island, some general points can be made, despite the limited data for nest-building on the island. All 7 subjects who were seen building nests on the island had a nest-buiding score of at least 4 (mean = 5.3) at the laboratory. For the 6 subjects not seen building nests on the island, it is possible that some of these subjects were building nests on the island, but had not been seen doing so. It is interesting to note, however, that the mean nest-building score at the laboratory for this group (3.8) is lower than the mean score for those seen building nests following release. The 3 subjects with the lowest nest-building scores were in this group, including *Maki*, the only subject seen sleeping on the ground following release.

Although all subjects showed some nest-building abilities at the laboratory, or at least an interest in branches if they could not get access to any, this did not automatically mean that they built nests in trees following release. The most prominent characteristic seen in nest-building at the laboratory was the action of forming a circle around the body with sticks or twigs. Forming a circle on the ground in this way, although it seems to be the most salient characteristic of nest-building, requires little skill, and is therefore unlikely to give an indication of a subject's ability to construct a functional sleeping platform in a tree.

Nest-building trials before release in a great ape release project such as this, are still recommended, however, particularly if access is given to platforms above ground-level to discourage sleeping on the ground; especially if release into an area with potential predators is planned, but also to decrease the likelihood of picking up external parasites from sleeping on the ground. If subjects were to be individually tested (so that all subjects can obtain enough nest-building materials), and if trials were repeated at regular intervals, these trials could also be a form of training before release. The trials, even though not entirely conclusive, can at least give an indication of each subject's nest-building abilities.

## SUMMARY OF ADAPTIVE BEHAVIOUR

The adaptive behaviours which developed following the release of Group 1 onto Island A are summarised in Table 5.4 (for subjects on the island for at least 1 month). The 3 subjects who became ill and died more than one month after release (*Maki, Daniel, Knut*) were subjects who in general did not learn some behaviours which required more skill, such as nut-cracking and ant-eating. That is not to say that they had to be able to crack nuts or eat ants in order to be able to survive on the island, but it may generally show that they were not adapting as well as the others.

In general, however, most of the group adapted well to the new environment, and if one subject showed an adaptive behaviour, this seemed to encourage the others to show the same behaviour, either as a result of observational learning, or by having memories of a previous ability prompted, or a combination of both. The spread of another behaviour through the group, tool-use for nut-cracking, is discussed more fully in the following chapter.

PAGE
NUMBERING
AS
ORIGINAL

**TABLE 5.4** Adaptive behaviour observed on Island A.

| | Name | Eats wild foods | Builds nests | Cracks nuts ** | Eats ants | On island >1m, <12m |
|---|---|---|---|---|---|---|
| A. | Maki | + | | | | 2m |
| | Daniel | + | | + | | 4m |
| | Knut | + | | | | 7m |
| B. | Hermaphrodite | + | + | + | + | 7m |
| C. | Blamah | + | + | + | + | |
| | Brutus | + | + | + | + | |
| | Carolla | + | + (*) | | | |
| | Goldilocks | + | | + | + | |
| | Grace | + | | + | + | |
| | Helen | + | + | + | + | |
| | Houdina | + | + | + | | |
| | Maria | + | + | + | + | |
| | Meryn | + | | + | | |
| | Popeye | + | | + | + | |
| | Samantha | + | + | + | + | |
| | Sokomodo | + | | + | | |

A - became ill and died
B - crossed canal and was killed by chimpanzees on adjacent island
C - survived on island for more than 1 year

* - ground nests only

** - see next chapter

# CHAPTER 6

## NUT-CRACKING

Some of the data presented in this section have been presented elsewhere (HANNAH & McGREW, 1987), however, further data and discussion are included here.

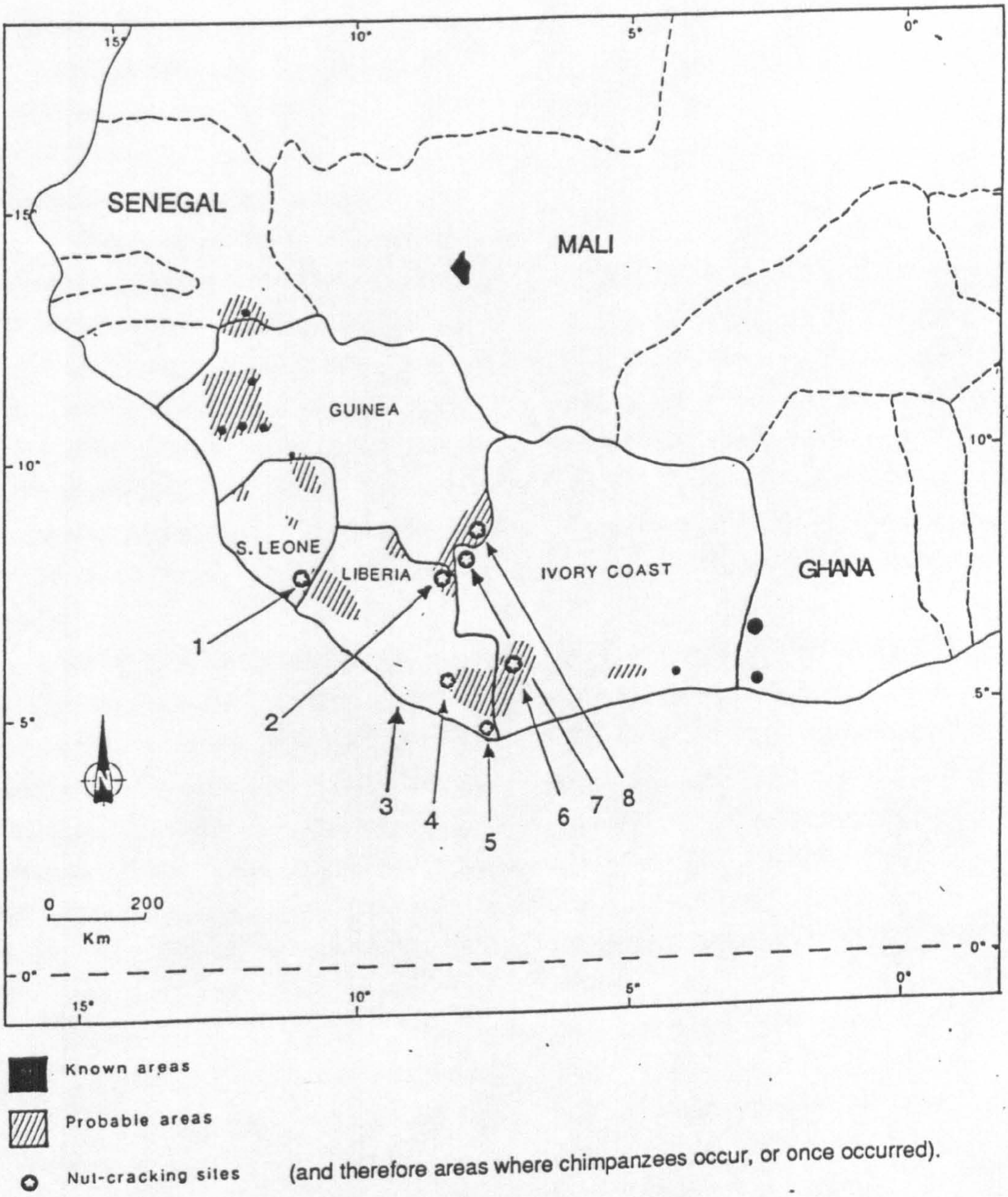
### Introduction

Evidence of wild chimpanzees (*Pan troglodytes*) using tools to open hard-shelled nuts comes from several locations in West Africa (Figure 6.1). SAVAGE & WYMAN (1844) reported nut-cracking by wild chimpanzees using hammer-stones in Liberia (the species of nut was not identified, but from the description given could possibly be *Coula edulis*). More direct evidence was then reported by BEATTY (1951), who saw an ape cracking palm nuts (*Elaeis guineensis*) on a rock anvil, using a stone as a hammer. Further evidence from Liberia was reported by ANDERSON et al. (1983), who found signs of chimpanzees opening four species of nuts (*Coula edulis, Panda oleosa, Parinari excelsa, Sacoglottis gabonensis*) on roots or surface rocks using hammer-stones.

STRUHSAKER and HUNKELER (1971) and RAHM (1971) found evidence of this type of tool-use in Tai Forest, Ivory Coast, where *Panda oleosa* and *Coula edulis* nuts were opened on surface roots with stone and wooden hammers. Direct observations of chimpanzees at Tai were made later, (BOESCH,1978; BOESCH and BOESCH 1981, 1983, 1984 a,b,c.) reporting five species of nuts (*Coula edulis, Panda oleosa, Parinari excelsa, Sacoglottis gabonensis, Detarium senegalense*) to be eaten, with stones or wooden clubs used as hammers on anvils of rocks, surface roots, or tree-branches. In a recent survey in the Mount Nimba Reserve, Ivory Coast (pers. obs.), one *Panda oleosa* cracking site with a stone hammer and anvil was found. This was the only cracking site found in a one month survey, perhaps because the chimpanzees only ranged within higher altitudes, where other nut-producing species did not occur.

Wild chimpanzees in Guinea (SUGIYAMA and KOMAN,1979; SUGIYAMA, 1981) and in Sierra Leone (WHITESIDES, 1985) also use nut-cracking tools. SUGIYAMA and KOMAN saw chimpanzees using hammer-stones and anvils to open palm nuts (*Elaeis guineensis*). WHITESIDES found evidence of probable tool-use for cracking *Detarium senegalense*, which was later confirmed when an ape was seen

**FIGURE 6.1** Distribution of Pan troglodytes verus in West Africa, and sites where nut-cracking has been reported.




(and therefore areas where chimpanzees occur, or once occurred).

Nut-cracking sites

1. Tiwai Island, Sierra Leone (WHITESIDES, 1985).
2. Mount Kanton, Liberia (KORTLANDT & HOLZHAUS, 1987).
3. Liberia (site unknown; BEATTY, 1951).
4. Sapo National Park, Liberia (ANDERSON et al, 1983).
5. Cape Palmas, Liberia (SAVAGE & WYMAN, 1843).
6. Tai National Park, Ivory Coast (STRUHSAKER & HUNKELER, 1971; RAHM, 1972; BOESCH & BOESCH, 1981, 83, 84).
7. Mount Nimba Reserve, Ivory Coast (FRUTH, JOULIAN & HANNAH, unpublished data).
8. Bossou, Guinea (SUGIYAMA & KOMAN, 1979; KORTLANDT & HOLZHAUS, 1987).

cracking these nuts on a surface root, using a stone as a hammer.

Recent evidence of stone tool-use for breaking open hard-shelled fruits of *Adansonia digitata* by wild chimpanzees in Mt. Asserik, Senegal, was reported by BERMEJO et al. (1989; see also BREWER, 1982 below for reports of stone tool-use by rehabilitated chimpanzees in the same area).

Stone tool-use for nut-cracking was also studied in two groups of chimpanzees who have spent much of their lives in captivity. SUMITA et al., (1985) first elicited tool-use for cracking walnuts (*Juglans* sp.) from chimpanzees caged alone. Then, they put 3 individuals who had acquired this tool-use habit together with 11 others in a setting with rocks and walnuts, in order to see if the technique would spread. The infants of the group showed interest, and one infant female who had closely watched walnuts being cracked with rocks later tried it. After some trial and error she was able to open walnuts in this way. SUMITA et al. believed that the adults of the group were not interested in the behaviour of the nut-cracking individuals, and that this explained why they did not acquire it.

BREWER (1982 : 350-354) reported another example of chimpanzees using stone tools, in a group released from captivity and being rehabilitated to living in a natural environment in the Niokola Koba National Park in Senegal. Younger members of the group learned to open pods of *Afzelia africana* and fruits of *Oncoba spinosa* using stones, although they rarely succeeded in opening *Afzelia* pods, which had to be positioned precisely. The two older members of the group, one male and one female, opened the pods with their canine teeth. The latter also hit the fruit of *Adansonia digitata* (baobab) against a branch or a stone without being shown how to do it, and the younger apes were then shown how to do this by BREWER.

Nut-cracking was first seen in my study group on 20 July 1985, when an adult female (*Samantha*) released on that day exhibited the behaviour. Nut-cracking behaviour was then shown by others, including 6 juveniles who had already been on the island for 6 weeks and 2 adolescents who had been on the island for 4 weeks. These 8 individuals had shown no interest in palm nuts or signs of tool-use before *Samantha's* release, even though the same raw materials were available. Later, all acquired this skill, suggesting that *Samantha*'s example had influenced their behaviour. Another adult female released on 20 July and three adolescent males released later also acquired the technique of nut-cracking, so that of the eventual group of 16, 13 were successful nut-crackers. The development of this behaviour will be discussed in the following sections.

Origin of nut-cracking

On 20 July 1985 at 1000 hours 3 females were added to the group of 10 chimpanzees already living on Island A. Later that day, at 1600 hours, one of these females, *Samantha*, was seen cracking palm nuts and eating the kernels. (There were many dried palm nuts lying naturally on the ground about the feeding-area). After collecting several nuts, she placed them, one at a time, on the small concrete stand supporting the water tap in the feeding area. She then hit these nuts with a concrete block held in one hand. It weighed 1.6 kg, and measured 11x13x4 cm. She did this skillfully, without prompting.

Human influence

Human intervention first took place 4 days after the first nut-cracking was seen. Four stones (2 hammers and 2 anvils, see below) were taken to the island. Stones were again taken to the island two weeks later and 10 weeks later. Two other chimpanzees had begun cracking nuts before the first stones were taken to the island and two more cracked nuts on that day. Further interventions were : collecting palm nuts, showing chimpanzees the sources of this collection (3 times), carrying nuts by hand to cracking sites (3 times), giving nuts to the apes to open (4 times), and, in 2 cases, opening nuts and allowing chimpanzees who had not yet been observed opening them to eat the kernel (once each for *Meryn* and *Hermaphrodite*). Apart from this, the author merely watched but did not teach the chimpanzees.

Spread of nut-cracking through the group

*Samantha's* nut-cracking at the feeding site attracted the attention of other chimpanzees within seconds (Figure 6.2), in particular *Goldilocks*. *Goldilocks* watched *Samantha* very closely, then picked up the hammer as soon as *Samantha* put it down and began to hit nuts on the concrete stand in the same way. *Goldilocks* succeeded in opening nuts, although she was more clumsy than *Samantha*, and tended to hit nuts too hard, breaking the kernel into many small pieces. Another younger female, *Popeye*, also opened nuts, and a fourth female, *Grace*, tried to open nuts but was unsuccessful. She put the nuts on the ground to hit them, so they got pounded into the ground and were not

FIGURE 6.2 Samantha cracking palm nuts, others watching.

opened. At this point there were 9 females and 3 males on the island, with the 3 remaining older males yet to be released.

On the following 2 days *Grace* again tried to crack nuts, this time on the wooden floor of the cage at the feeding area. She still failed, apparently because she was not hitting the nuts hard enough. Apart from this, no other nut-cracking was seen in 12 hours of observation over the 3 days following Samantha's first nut-cracking.

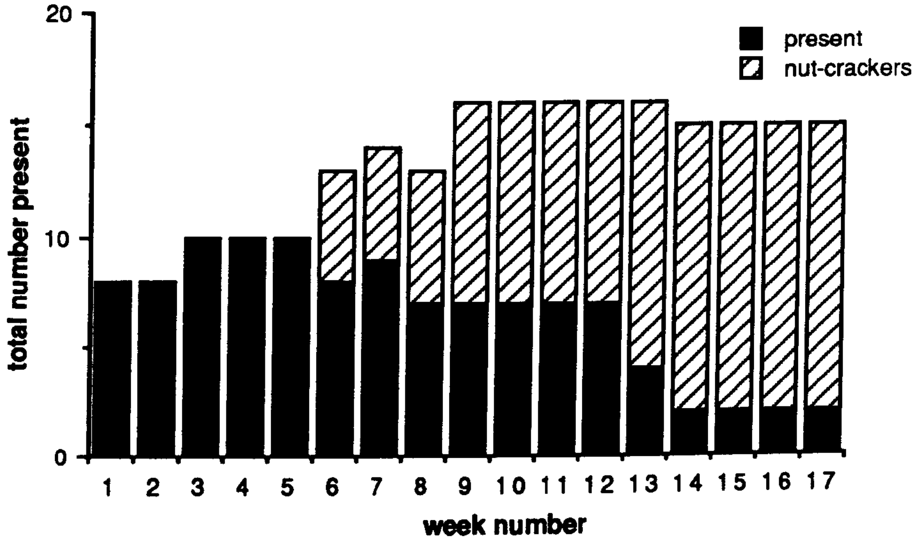
The observer then took 2 stones (each weighing 1.5kg) and 2 large concrete slabs (weighing about 15kg each) to Island A, intending the stones to be used as hammers and the concrete slabs as anvils. This was the first human intervention in the nut-cracking. The stones and slabs were placed at the feeding area. The first individual to use one of these stones was *Samantha*, who cracked nuts on the concrete tap stand. *Goldilocks* then used the other stone to crack nuts on a concrete slab. *Meryn* then tried to crack nuts. He made many mistakes, such as hitting an empty piece of shell, missing the nut, or holding a nut in his hand and hitting it against the concrete slab, but he persisted until he managed to open nuts and eat the kernels. *Houdina* was skillful at opening nuts the first time she was seen to do so. *Grace* again tried but failed to crack nuts on the wooden floor of the cage.

On 7 August *Samantha* had a baby and showed less interest in nut-cracking for the next few weeks. However, 4 other individuals were by then using stones to crack nuts, and the habit continued to spread through the group (Figure 6.3). For example, 3 weeks after the first nut-cracking observation, *Goldilocks* arrived at the feeding site with a handful of nuts, which she began to open. *Blamah* watched her very closely (Figure 6.4), and then she too opened some nuts. Although this was the first time she had been observed to do so, she was quite skillful.

Within a month of the first nut-cracking observation, 9 of the 13 chimpanzees in the group cracked palm nuts using stones. Of the 4 remaining subjects, 3 still did not acquire this ability in the following three months. Of these 3, *Knut* showed interest and often managed to eat kernels of nuts opened by *Hermaphrodite*, his close companion, but he never was seen to try to crack nuts. The other two, *Maki* and *Carolla*, seemed less interested, although both were seen stealing kernels of nuts opened by others. *Maki* only stole kernels when nut-cracking first began (however, she was removed from Island A two months later), whereas *Carolla* was still occasionally seen stealing kernels in the following months.

The 3 older males (*Daniel, Sokomodo, Brutus*) released 25 days after the first

**FIGURE 6.3** Spread of nut-cracking behaviour through group.




present = subjects present on island who have not been seen cracking nuts
nut-crackers = subjects on island who have cracked nuts

week number = week following release of first sub-group

**FIGURE 6.4** Blamah watching Goldilocks cracking palm nuts.

nut-cracking observation all acquired the skill. For the first 2 weeks that these 3 males were on the island, there were no observations in the interior of the island. During this fortnight of more limited observations, *Goldilocks, Blamah*, and *Helen* brought nuts a few times to the feeding site to open, but the 3 males had not yet been seen cracking nuts (although there were 2 other cracking sites which the author did not visit during this fortnight). The author then gave some nuts to *Daniel* when he was sitting next to some stones at the feeding site. He took the nuts and opened them with the stones, although his method was a little clumsy. Four days later, when the author was walking around the island, *Sokomodo* was observed cracking nuts at a site in the interior of Island A, and 5 days later *Brutus* was also observed cracking nuts.

New nut-cracking sites

Three weeks after the first nut-cracking was seen, the author took 4 stones (2 hammers and 2 anvils) to another part of Island A. They were put next to a palm tree with many nuts below it and not far from other palm trees with nuts around them. The group of chimpanzees followed and as soon as the stones were put down, *Samantha* and *Grace*, the two top-ranking females, collected handfuls of nuts and sat breaking these, not allowing any of the others who were gathered around to eat the kernels or use the hammer-stones. Each time *Samantha* ran out of nuts, she collected more in one hand, while keeping the hammer-stone in the other. When *Grace* ran out of nuts she collected more from 2-3 m away, leaving the hammer stone on the anvil and collecting nuts in both hands. Some of the others sat next to the hammer-stone and anvil, but they did not attempt to use them while *Grace* was collecting more nuts. *Samantha* and *Grace* continued opening nuts, then Popeye took over the hammer-stone *Grace* had been using while she was again collecting nuts. *Popeye* carried this stone to a fallen tree trunk 3 m away which she used as an anvil. *Grace* returned with nuts and searched around the anvil for the hammer-stone which she had been using. *Popeye* was within sight but *Grace* did not attempt to take back the hammer-stone from her. (She might well have done so if *Popeye* had been using the hammer-stone at the same place where *Grace* had left it). Instead, *Grace* took her nuts and sat next to *Samantha* until she got a chance to take over *Samantha's* stone, then she cracked her nuts.

The second nut-cracking site became well used (Figure 6.5). When the chimpanzees were going round the island they often stopped to use the stones to crack nuts, which they often started to collect when the stones were not in sight.

**FIGURE 6.5** Chimpanzees around a cracking site on Island A.

Ten weeks after the first nut-cracking was seen, the author took another 4 stones (2 hammers and 2 anvils) to a third site on the island. The chimpanzees followed, and seemed to expect that these stones would be put down for them to crack nuts with, because each time the observer passed an area with many palm nuts, they became excited and watched closely. When a suitable area (i.e. with nuts around and a small, level clearing) was found the stones were put down, and *Samantha* and *Grace* immediately began cracking nuts, not allowing the others to use the stones. (*Grace* attacked *Sokomodo* for using a hammer-stone while she was collecting more nuts - see below). Eventually *Grace* and *Samantha* left the stones and the others got a chance to crack nuts. The third site was not in an area often used by the chimpanzees but it became so. They remembered where the stones were and often went there to crack nuts.

Three weeks after the first nut-cracking observation, a cracking-site was found by the author on Island B, while looking for *Brutus* who had just been released and had disappeared. A large rock with a stone on top and nut shells all around was found 3 m from a palm tree. The large rock was partially sunk in the ground and the stone had been sitting 1m from the rock, as could be seen from a hole left in the ground when it was moved. This site was not used as much as the other nut-cracking sites because the chimpanzees did not often go to Island B. Eight weeks later, when 3 chimpanzees (*Goldilocks, Hermaphrodite*, and *Knut*) had travelled from Island A to Island B, a second hammer-stone and more nut shells were found at this site, and *Goldilocks* was seen cracking nuts at the site.

<u>Social interactions</u>

At nut-cracking sites, many social interactions between individuals were recorded, both aggressive, such as fighting over the use of hammer-stones, and affiliative, such as the sharing of nuts (Figure 6.6).

One example of aggression at a nut-cracking site occurred when *Sokomodo* took over a hammer-stone which *Grace* had just been using, while she was 2-3 m away with her back to him. *Grace*, on returning to see *Sokomodo* using the stone, screamed and jumped at him, then slapped him. *Sokomodo* immediately dropped the stone and moved away. When *Grace* went to collect nuts for a second time, *Sokomodo* again used the stone she had just put down. This time when Grace returned, she seemed even more upset than before, and she attacked *Sokomodo*, who ran off screaming. *Grace* pursued

**FIGURE 6.6** Brutus reaching for the kernel of a nut Sokomodo has cracked.

him for over 30 m until they were both out of sight, before she returned to crack nuts again. *Sokomodo* returned after a short time but did not try to crack nuts until the others had left the nut-cracking site.

There were also many cases of sharing and stealing of nuts at cracking sites. For example, *Helen* always allowed *Maria*, her close companion, to eat kernels of nuts that she had just opened. Once when *Helen* was cracking nuts, watched by *Maria* and *Meryn*, *Helen* continually allowed *Maria* to take kernels from the anvil, but each time *Meryn* reached toward the anvil, she slapped his hand. *Meryn* became more upset each time this happened and eventually left.

When one individual tried to take nuts from an anvil, or directly from the hands of another individual who had just collected them, the reaction varied according to the individuals concerned and to their rank in the group. Responses varied from handing over all of the nuts just collected, to giving over some nuts then moving to another stone, to turning away and ignoring the individual trying to take nuts. The following incident involved both attempted stealing of nuts and then sharing of nuts. *Hermaphrodite* arrived at the feeding site with a handful of nuts and sat down at some stones to crack them. However, *Sokomodo*, who had been watching him from about 4 m away, then approached, presumably to take *Hermaphrodite's* nuts, which he often did. *Hermaphrodite*, however, on seeing *Sokomodo* approach, sat with his arms folded, hiding the nuts in his hands. Then, when *Goldilocks* (a frequent companion), finished cracking nuts with some stones nearby, *Hermaphrodite* approached her and held out his handful of nuts. *Goldilocks* took these and began to open them, allowing *Hermaphrodite* to eat some kernels. *Sokomodo* watched them from about 2 m away, but did not approach or try to take the nuts.

Transport of nuts and hammer-stones

As the chimpanzees used up the nuts that were lying on the ground around the feeding site they began to bring nuts from other areas on the island, carrying them in the mouth, in their hands, or both. The author collected nuts on 24 July 1985. These nuts were about 150m from the feeding site which was out of sight. *Samantha* and *Goldilocks* both watched the observer collecting these nuts and then they collected nuts in their hands and took them to the feeding site where they opened them to eat. This was the first observation of nut-carrying. Following this, the chimpanzees were observed carrying nuts many times. Distances nuts were carried were not always verified, but at least once, *Goldilocks* carried nuts a distance of 265m, passing an alternative nut-cracking site on the way and taking them to the feeding site to open. It was more common, however, for subjects to carry nuts to the cracking site nearest the collecting point. Sometimes subjects made successive trips around the island to collect nuts which they brought to the feeding site to open. For example, *Helen* once made five nut-collecting trips within one hour, and *Hermaphrodite* once made eight nut-collecting trips within two hours. The chimpanzees also began to climb palm trees to collect nuts as well as collecting nuts which had already fallen.

Nuts were usually carried in one hand (N=39), but also in the mouth (N=11), the mouth and both hands (N=4), the mouth and one hand, (N=8) or least often, in both hands only (N=2). The type of carrying varied with the distance being travelled. A subject sometimes started by carrying nuts in the mouth, then transferred them to one hand. This often happened when the subject stopped to eat leaves on the way to the cracking site, thus the mouth was freed. *Blamah* once stopped, moved nuts from her mouth to her hand, ate some leaves, put the nuts back into her mouth, then moved on. Usually, however, once nuts were taken from the mouth they were then carried in one hand. When subjects carried nuts in their hands, this did not affect locomotion, unless nuts were being collected from palm trees, in which case hands had to be free for climbing and so nuts were carried in the mouth. Up to about 6 nuts could be carried in one hand, and the same in the mouth.

As well as carrying nuts around the island, it became apparent that the chimpanzees were also moving hammer-stones from one area to another. Some 'new' hammer-stones were found at cracking sites, i.e. ones which the chimpanzees had found and taken there, or marked hammer-stones which had been left in one area by the observer were moved to another area. The heaviest hammer-stone moved weighed 2.6kg and was carried a distance of at least 175m.

Use of surface-roots as anvils

Wild chimpanzees often use tree surface-roots as anvils (eg. ANDERSON et al., 1983; BOESCH & BOESCH, 1984 a; WHITESIDES, 1985), which means that if they can carry a hammer-stone to an area where there are nuts, they can then find a suitable surface-root nearby to use as an anvil (often these are surface-roots of the nut-producing tree - pers. obs.). The island chimpanzees in this study , however, throughout the first island study period were seen using mainly stone anvils, apart from an occasional observation of *Popeye* using a fallen tree-trunk as an anvil. On the first day she was released during island study period 2, however, the adult female *Grace* used a surface root of a tree at the feeding site as an anvil. At this point there were 10 chimpanzees on the island, 9 of whom could crack nuts (*Carolla* never having been seen doing so). Six of these chimpanzees had already been on the island 4 days before *Grace* was released. On her second day of release (i.e. 3 days before *Grace* was released), *Maria* was seen attempting to crack a nut on a surface-root in the interior of the island. The root was damp and soft, however, so she was unsuccessful in cracking the nut. The next day, *Maria* was seen putting nuts onto the surface root *Grace* later used, but when the nuts rolled off she did not persist and used a concrete anvil at the feeding site. Other observations (N = 8) of nut-cracking before *Grace* was released were all on stone anvils.

On the afternoon *Grace* began using a surface-root at the feeding site as an anvil, nut-cracking continued for the following 2 hours and involved the 8 other subjects who could crack nuts. After *Grace* had begun using one surface-root, *Houdina* then used another surface-root of the same tree, 1m from the one *Grace* used. During the following 2 hours, *Helen* and *Samantha* also used these 2 roots as anvils. There were only 2 hammer-stones at the feeding site, which were used almost continually by the 8 nut-crackers for the 2 hours. Each time one chimpanzee put down a hammer-stone and left to collect more nuts, another took the stone and used it. These 2 stones were moved continually between the 2 surface roots being used as anvils and 3 concrete anvils at the feeding site. The shortage of hammer-stones also resulted in *Popeye* attempting to use a stick as a hammer. The stick was 1m long and 4 cm in diameter. *Popeye* used the stick in an upright position, like a mortar (unlike Tai chimpanzees which use sticks in a horizontal position, BOESCH & BOESCH, 1984). *Popeye* was unsuccessful in opening the nut, and put the stick down. Meryn then attempted to use the stick, holding it horizontally. He was also unsuccessful, however. This may be due to the fact that the stick was too narrow. Tai chimpanzees use sticks greater than 5cm in diameter, which are therefore heavier. The stick was not too long, since Tai chimpanzees can use sticks much longer than 1m (pers. obs.), using them in a lever-like manner.

Two hours after nut-cracking began, the surface-roots had clear depressions which nuts could be placed in without rolling off, and had large areas (10 cm) along the roots which were stripped of bark. One afternoon of use could therefore produce a recognisable cracking-site.

Following this observation, other surface roots on the island were used as anvils, which allowed the chimpanzees to crack nuts in many more locations.

Learning of nut-cracking by members of Group 2

In February 1986, when 5 members of Group 1 were housed together with 10 members of Group 2 (Table 6.1), the opportunity was taken to study the learning of nut-cracking by these 10 new group members. First, the members of Group 1 (plus *David* of Group 2, who went into the separating cage at the same time) were separated from the members of Group 2 who were then given nuts and stones to see if any subjects would spontaneously crack nuts. The members of Group 2 did not show any signs of nut-cracking behaviour, even when the author cracked a nut on a window ledge of the enclosure where they could clearly watch. They did not show very much interest in the nuts or stones.

The 5 members of Group 1 were then let back into the enclosure, and immediately began to crack nuts. Thirty minutes later, *David* of Group 2 began to crack nuts, without showing any errors. At the same time, *Twebo* also tried to crack some nuts with a stone, but did not appear to hit them hard enough. One hour later, *Twebo* was seen holding a nut in her hand and hitting it against a hammer-stone, and 3 hours later she successfully cracked nuts open, using a hammer-stone held in each hand (Figure 6.7). From the time Group 1 was let back in, the subjects were observed for the following 2 hours. During this time, 1 member of Group 2 (*David*) cracked nuts and 4 others (*Twebo, Moffit, Bill* and *Natasha*) showed some components of nut-cracking behaviour (see Table 6.1). The kinds of errors shown in unsuccessful attempts to crack nuts were : holding a nut in the hand and hitting it against a stone, hitting a nut with a fist, and hitting a nut with a stone on the sand floor of the enclosure (Figure 6.8).

Two hours later, another supply of nuts was given out. *Twebo* successfully cracked nuts, and one more member of Group 2 (*Mabel*) also tried to crack nuts.

One week later, when nuts were provided again, the same results were found, that is, all 5 members of Group 1 cracked nuts, 2 members of Group 2 cracked nuts, and 3 members of Group 2 showed some components of nut-cracking behaviour, but did not succeed. It appeared, however, during both these trials, that members of Group 2 were limited by the number of nuts they could obtain because the 5 members of Group 1 each collected handfuls of nuts for themselves, and were also seen taking nuts from members of Group 2 when their nuts were finished. Some members of Group 2 seemed afraid to take any nuts at all, because they had been chased away from the nuts when they were first put into the enclosure.

The next nut-cracking trial for members of Group 2 was therefore postponed for 2 months until June 1986, following the transfer of all members of Group 1 (except for *Meryn*) into another enclosure. Then, when nuts and stones were again provided, 4 females of Group 2 (*Bertha, Moffit, Natasha, Tipsy*) who had not managed to crack nuts before, now successfully cracked nuts (Table 6.2). The 5 new additions, however, did not show any signs of nut-cracking behaviour.

In May 1987, when 25 subjects were housed together in 2 enclosures with a passage between them (Figure 2.11), further nut-cracking trials were carried out. Data were collected by the author and Mary Richardson, one observer watching each enclosure. During trials on 3 consecutive days, all but one member of Group 2 (*Wolfram*) showed some components of nut-cracking behaviour (Table 6.3). Five males of Group 2 (*Bill, Jimbo, Mango, Saffa, & Wolfram*) did not successfully crack nuts, but the other 13 members of Group 2 managed to crack nuts (Figure 6.8). *Carolla* of Group 1, who had never been seen cracking nuts on Island A, also did not crack any nuts at the laboratory. (*Carolla*, however, was seen cracking nuts in March 1989, almost 4 years after she first had the opportunity to learn the behaviour).

Discussion on origin and spread of nut-cracking behaviour

Eight of the 10 chimpanzees living on the island before *Samantha's* release showed no interest in palm nuts and never tried to open them until *Samantha* did. Nor did these 8 resident apes climb palm trees to collect palm fruits in order to eat the outer husk. After *Samantha's* demonstration, the 8 began cracking palm nuts. This sequence of events suggests that they acquired the nut-cracking technique by observation, or had their memories prompted by her actions. Some individuals took many trials to learn and made errors, whereas others began immediately without making any errors.

BECK (1976, 1980) proposed 3 ways in which observation of others may influence an individual's behaviour. The first is *social facilitation*, that is, exposure to a model may increase the overall activity of the observer which in turn can facilitate trial and error learning by causing trials to be produced more rapidly. The second, *stimulus enhancement*, may cause the observer to be more likely to manipulate the tool, and therefore increase the likelihood of the observer discovering the solution by trial and error. The third possibility involves observation, then performance of the appropriate behavioural pattern, without any trial and error, by *imitative copying*.

TOMASELLO et al. (1987), in a study of the acquisition of tool-use by captive chimpanzees (by using a T-bar to obtain food out of reach), found that their results did not fit directly into any one of BECK's (1980) categories. They proposed that the most

**TABLE 6.1** Nut-cracking at laboratory, February 1986.

| | Name | Succesful in cracking nuts | Showed some components of nut-cracking behaviour | Comments |
|---|---|---|---|---|
| Group1 | Blamah | + | | |
| | Helen | + | | |
| | Maria | + | | |
| | Meryn | + | | |
| | Popeye | + | | |
| Group 2 | Anita | | | |
| | Bertha | | | |
| | Bill | | + | hit stone against concrete shelf, but did not have nut |
| | David | + | | no errors |
| | Mabel | | + | hit nut with stone, but did not open it |
| | Moffit | | + | hit nut with stone, then Popeye took nut from her |
| | Natasha | | + | hit nut with concrete flake; held nut in hand & hit on floor |
| | Tipsy | | | |
| | Tolkein | | | |
| | Twebo | + | | hit nut with stone, but not hard enough; held nut in hand and hit against hammer-stone; successful 2 hours later |

Subjects are listed alphabetically within groups.

**TABLE 6.2** Nut-cracking at laboratory, June 1986.

| | Name | Succesful in cracking nuts | Showed some components of nut-cracking behaviour | Comments |
|---|---|---|---|---|
| Group1 | Meryn | + | | |
| Group 2 | Anita | | | |
| | Bahnti * | | | |
| | Bertha | + | | *after cracking* nut with no errors, then hit nut on sand; then moved back to solid base |
| | Big Sore * | | | |
| | Bill | | + | hit stone against concrete shelf, but did not hit nut |
| | Dr. Me * | | | |
| | Mabel | | + | |
| | Moffit | + | | |
| | Natasha | + | | |
| | Telle * | | | |
| | Tipsy | + | | |
| | Tolkien | | + | hit stone against concrete shelf, but did not hit nut |
| | Twebo | + | | |
| | Wolfram * | | | |

Subjects are listed alphabetically within groups.

* - members of Group 2b (Table 2.3) added to enclosure since last nut-cracking trial, i.e., had not seen other subjects cracking nuts before.

**TABLE 6.3** Nut-cracking at laboratory, May 1987.

| | Name | Succesful in cracking nuts | Showed some components of nut-cracking behaviour | Comments |
|---|---|---|---|---|
| Group1 | Blamah | + | | |
| | Carolla | | | took kernels from Meryn |
| | DmW | + | | |
| | Helen | + | | |
| | Houdina | + | | |
| | Maria | + | | |
| | Meryn | + | | |
| Group 2 | Anita | + | | no errors |
| | Bahnti | + | | no errors |
| | Bertha | + | | |
| | Big Sore | + | | first hit nut with hand |
| | Bill | | + | hit nut against a stone |
| | David | + | | |
| | Dr. Me | + | | |
| | Jimbo | | + | stole & eat kernels; hit stone on ledge, but no nut; spinned with stones & threw them |
| | Mabel | + | | |
| | Mango | | + | eat others kernels, hit nut with a very small stone |
| | Moffit | + | | |
| | Natasha | + | | |
| | Saffa | | + | hit 1 stone with another |
| | Telle | + | | no errors |
| | Tipsy | + | | no errors |
| | Tolkien | + | | |
| | Twebo | + | | |
| | Wolfram | | | eat others kernels |

Subjects are listed alphabetically within groups.

**FIGURE 6.7** Twebo cracking palm nuts at laboratory.

**FIGURE 6.8** Natasha hitting a nut on the sand.

plausible explanation for their results was a variation of the *stimulus enhancement* hypothesis, since the chimpanzees did not just learn that some objects were of special interest, but rather that some objects had a special utility in their use as tools. Observation of a model showing the appropriate behaviour helped experimental subjects learn not just to manipulate the tool (which was also done by control subjects who did not observe the model showing the appropriate behaviour), but to use the tool-object in its function as a tool.

Some data are available for first observations of nut-cracking by some subjects on the island in the present study. For example, in the case of *Goldilocks* and *Popeye*, who observed *Samantha* and then immediately cracked nuts without any trial and error, their behaviour may have been direct *imitative copying* of *Samantha's* behaviour, whereas *Meryn*, who first showed trial and error, may have arrived at the solution through *stimulus enhancement* (or a revised version of *stimulus enhancement* proposed by TOMASELLO et al., 1987). For most other subjects, the first time they were seen cracking nuts, they did so successfully. This was sometimes weeks after the first nut-cracking observation, however, and it was not known if they had first shown errors, perhaps when the author was not present. Little can be said, therefore, about how they learned the behaviour. Following the return of Group 1 to the laboratory, during laboratory study periods 2 and 3 (Figure 2.4), when members of Group 2 were introduced, the development of nut-cracking behaviour by members of Group 2 was observed (see below for discussion).

The question of when and where *Samantha* (who was first seen cracking nuts on the day she was released) learned this behaviour is less clear. The chimpanzees at the laboratory were frequently fed palm fruits, so that all chimpanzees in the group were familiar with palm nuts before arrival on the island. Some cages at Vilab had concrete floors; other large enclosures had only sand floors, but these had shelters with concrete bases. The chimpanzees thus had a firm base upon which to crack palm nuts, but they did not have any hard objects which could serve as hammers and so as far as the author could determine, they had never been seen cracking nuts before release.

There are at least 2 possibilities which might explain where *Samantha* learned the technique for cracking nuts. The first is that she had retained some memory of this behaviour from her one year in the wild. Infant chimpanzees show interest in nut-cracking when they are less than one year old, but usually do not crack nuts themselves until they are about 3 years old (pers. obs.). The second possibility is that *Samantha* learned or developed the technique for nut-cracking from a human caretaker.

*Samantha* was young on arrival at the laboratory and for almost 2 years was taken care of by human caretakers. Human caretakers at the laboratory took infant chimpanzees outside most days. In 1986, the author saw 2 such caretakers with 4 young chimpanzees sitting outside and cracking palm nuts with stones to eat the kernels. The chimpanzees were interested in their behaviour, and the caretakers gave then some kernels to eat. Perhaps *Samantha* learned or developed the technique for cracking nuts through similar observation of a human caretaker.

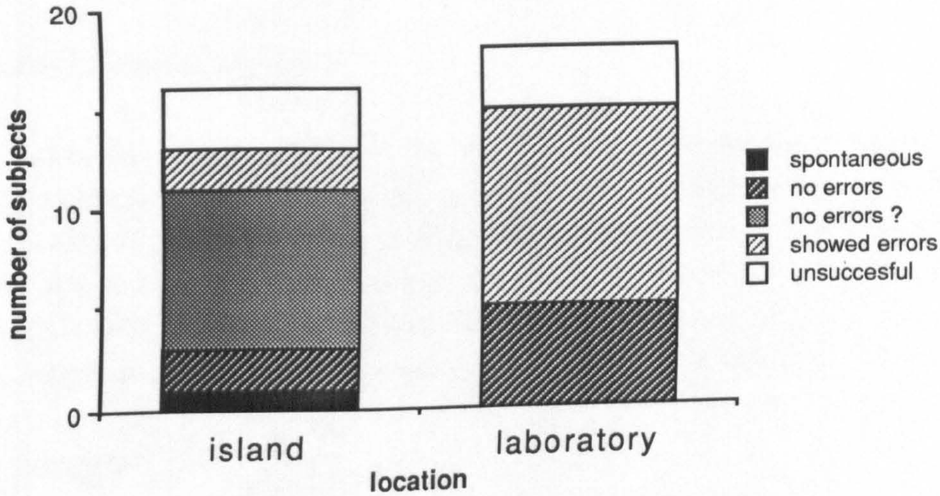
Summary of nut-cracking by Group 1 and Group 2

When data from members of Groups 1 and 2 who were present during nut-cracking studies either on Island A or at the laboratory are combined, this gives data for a total of 35 subjects (Figure 6.9). At the laboratory, as was found on the island, some subjects began to crack nuts without showing any trial and error, whereas some first made errors, then learned the correct technique. The data from both the island and the laboratory therefore suggest that two different learning processes may be involved. Some subjects appeared to show direct *imitative copying* of others' behaviour, whereas others seemed to perceive the goal of opening the nut, but arrived at the correct technique through trial and error; that is, some form of *stimulus enhancement* may have been involved.

When the nut-cracking behaviour of males and females in both groups is compared (Figure 6.10), there is a trend for females to be more successful in cracking nuts, although this difference is not significant (Fisher's exact probability, $p = 0.07$). Sex differences in tool-use have been found in wild populations of chimpanzees (McGREW, 1979; BOESCH & BOESCH, 1984 b), with females either being more proficient tool-users, or being involved in tool-use behaviours more frequently than males.

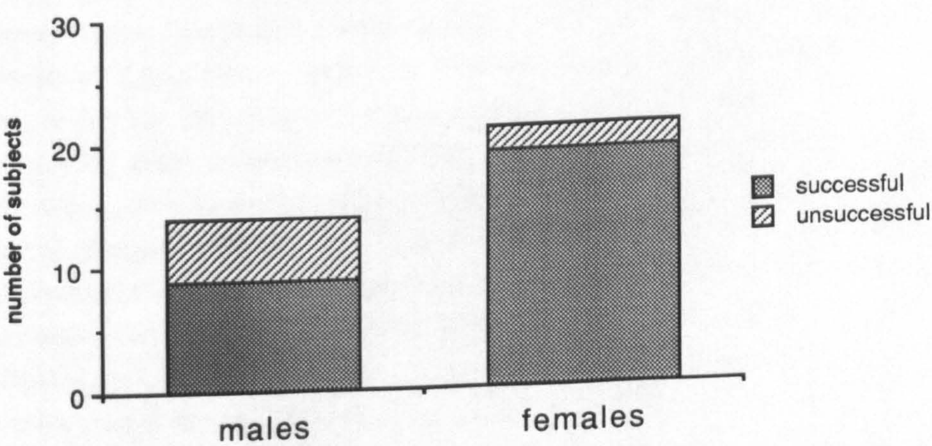
For all subjects in the present study, the possibility that they had prior experience of nut-cracking before capture cannot be excluded. As more wild populations of chimpanzees are studied and more data becomes available, the number of sites in West Africa where wild chimpanzees are known to crack nuts is increasing. It is therefore likely that many if not all of the chimpanzees in the present study, came from wild popualtions where nut-cracking occurred. This would explain why more subjects in this study successfully cracked nuts in comparison to other studies (SUMITA et al., 1985; THIEL, pers. comm.). More comparisons between wild-born and captive-born chimpanzees raised in similar environments, and perhaps also between wild-born subjects from different sub-species (some from areas where nut-cracking is not known to occur), would be necessary to investigate further the role of prior experience in the wild, even at an early stage, on the later development of a behaviour such as nut-cracking.

**FIGURE 6.9** Development of nut-cracking on island and at laboratory.




*spontaneous = spontaneously cracked nuts with no prompting*
no errors = did not show any errors before successfully cracking nuts
no errors ? = did not show any errors when author was present
showed errors = seen to make some errors before successfully cracking nuts
unsuccessful = did not learn to crack nuts

**FIGURE 6. 10** Learning of nut-cracking behaviour by males and females.




successful = learned to crack nuts; unsuccessful = did not learn to crack nuts

# CHAPTER 7

## SOCIAL AND STEREOTYPED BEHAVIOUR AFTER RELEASE

### Social Behaviour on Island A

Following release onto Island A, the fact that study subjects were in a larger group than in captivity, and could range freely in a larger area, affected their social behaviour. It was possible for subjects to split into subgroups for travel, easier to avoid aggressive encounters, and each individual had a larger choice of partners for social grooming, social play, and sexual behaviour. These categories of social behaviour will be discussed in the following sections, with comparison to behaviour at the laboratory where possible.

#### Subgroups

In the wild, *communities* (GOODALL, 1968) or *unit groups* (NISHIDA, 1968) of chimpanzees split into smaller groups which are " a temporary association of individuals that may be constant for a few hours or days" (GOODALL, 1968 : 211). These temporary associations have been called *groups* (GOODALL, 1968), *bands* (REYNOLDS & REYNOLDS, 1965), *subgroups* (NISHIDA, 1968), and *parties* (TUTIN et al., 1983). In the following sections, the term *subgroups* shall be used to describe such temporary associations.

On the author's arrival at Island A in the morning (8.00-9.00 hrs) and sometimes also for a second time in the afternoon (13.00-14.00 hrs), the study group usually arrived in separate subgroups at different times and from different directions. If subjects did not arrive within 1 hour after the author's arrival at the island, the author looked for them (if it was within the first month of release), or continued with other activities, such as provisioning then walking around the island. All subjects usually arrived for provisioning, with the exception of consort pairs (see below). If subjects arrived from different directions (from 1 of 3 different paths which led into the feeding area, approximately 90° apart), or from the same direction but more than 5 minutes apart, they were recorded in the separate subgroups in which they arrived. If subjects were already at the feeding area when the author arrived, no data were recorded for these subjects since it was not known if they had been travelling together or had met at the feeding area.

As each subgroup arrived at the feeding area, various types of greetings were observed. Greeting behaviour, as described by GOODALL (1968 : 284, 1986 : 366), consisted of many postures and gestures, such as : bobbing, bowing and crouching, touching, kissing, embracing, grooming, presenting, and mounting.

Travelling companions

From data on arrival in separate subgroups, the percentage of times each individual was recorded travelling in a subgroup with each other individual was calculated (excluding days in which one of the pairs of individuals being compared was not present). These percentage scores are listed in Tables 7.1 and 7.2.

Each individual seems to show a preference for travelling with 1 or 2 other individuals, the most striking pair being *Maria* and *Helen*, who were recorded together on 98% of samples in 1985, and 100% of samples in 1986. NISHIDA (1979) reported a case of 2 adolescent females who almost always travelled together for 1 year. *Maria* and *Helen* had been kept together for a number of years at the laboratory, as had *Meryn* and *Blamah*, who also showed a preference for travelling together (89% of samples in 1985, and 87% in 1986). Some pair preferences developed between individuals who had not been kept together before release, such as *Hermaphrodite* and *Goldilocks*, or *Houdina* and *Popeye*. *Houdina* and *Popeye's* preferences changed in 1986, however. *Hermaphrodite* was not on the island in 1986, and so *Goldilocks'* preferred companion cannot be compared between the 2 years. The most frequent travelling companions for each subject are listed in Table 7.3. Out of 10 subjects who could have shown the same travelling companion preference in 1985 and 1986, 7 did, indicating a trend for consistency in preferred travelling companion over the 2 years.

NISHIDA (1968) calculated the degree of inter-individual familiarity (calculated from the number of times individuals were recorded together, corrected for differences in the number of times different individuals were observed) for a unit group of wild chimpanzees. The values obtained showed that individuals had preferences in travelling companions.

The mean scores for each age/sex class from NISHIDA'S (1968) data and Island A data in 1985 and 1986 are illustrated in Figure 7.1. From his data, NISHIDA (1968 : 197) presented 2 statements about the social bonds within the unit group as a whole :

1) *"social bonds are stronger among adult males"*
2) *"male-female familiarity is stronger than female-female familiarity"*.

The first of these is true for the Island A data in 1986, but in 1985 bonds were stronger among adolescents. This stronger bonding among adolescents in the study

**TABLE 7.1** Individual choices in travelling companions, Island A, 1985.

| | D | Br | Hp | K | Mn | So | Bl | C | Dw | Go | Gr | Hl | Hd | Mk | M | Po | S |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| males | | | | | | | | | | | | | | | | | |
| Daniel (D) | - | 47 | 18 | 22 | 24 | **60** | 22 | 16 | 0 | 18 | 42 | 20 | 44 | 47 | 20 | 42 | 43 |
| Brutus (Br) | | - | 24 | 24 | 22 | **56** | 27 | 18 | 0 | 31 | 38 | 29 | 33 | 46 | 27 | 47 | 23 |
| Hermaph. (Hp) | | | - | 85 | 48 | 11 | 54 | 31 | 15 | **87** | 28 | 50 | 38 | 51 | 48 | 57 | 33 |
| Knut (K) | | | **85** | - | 48 | 31 | 60 | 31 | 15 | 67 | 29 | 57 | 45 | 57 | 51 | 61 | 31 |
| Meryn (Mn) | | | | | - | 27 | **89** | 30 | 12 | 46 | 29 | 60 | 59 | 46 | 61 | 57 | 36 |
| Sokomodo (So) | **60** | | | | | - | 29 | 18 | 20 | 24 | 51 | 20 | 44 | **60** | 20 | 53 | 36 |
| females | | | | | | | | | | | | | | | | | |
| Blamah (Bl) | | | | | **89** | | - | 33 | 12 | 49 | 31 | 56 | 59 | 43 | 56 | 58 | 35 |
| Carolla (C) | | | | | | | | - | 13 | 27 | 17 | 29 | 33 | 31 | 27 | **36** | 20 |
| DmW (Dw) | | | | | | | | | - | 12 | 12 | 19 | 15 | 8 | **23** | 15 | 16 |
| Goldilocks (Go) | | | **87** | | | | | | | - | 35 | 46 | 45 | 51 | 44 | 58 | 38 |
| Grace (Gr) | | | | | | | | | | | - | 26 | 49 | 40 | 25 | 45 | **53** |
| Helen (Hl) | | | | | | | | | | | | - | 45 | 43 | **98** | 50 | 40 |
| Houdina (Hd) | | | | | | | | | | | | | - | 57 | 42 | **71** | 62 |
| Maki (MK) | | | | | **60** | **60** | | | | | | | | - | 43 | 54 | 37 |
| Maria (M) | | | | | | | | | | | | **98** | | | - | 48 | 38 |
| Popeye (Po) | | | | | | | | | | | | | **71** | | | - | 51 |
| Samantha (S) | | | | | | | | | | | | | **62** | | | | - |

Notes

1) Scores represent the % of samples in which each individual was recorded in the same sub-group as each other individual (from the total no. of samples they could have been recorded together.
2) Scores from columns in the top-right of the table are not repeated in the bottom-left of the table unless (3).
3) In each row, the highest score(s) for that individual is (are) highlighted (two if equal).

**TABLE 7.2** Individual choices in travelling companions, Island A, 1986.

| | Br | Mn | So | Bl | C | Go | Gr | Hl | Hd | M | Po | S |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| males | | | | | | | | | | | | |
| Brutus (Br) | - | 57 | **85** | 68 | 51 | 66 | 57 | 53 | 50 | 53 | 70 | 62 |
| Meryn (Mn) | | - | 57 | **87** | 54 | 68 | 65 | 57 | 63 | 57 | 65 | 72 |
| Sokomodo (So) | **85** | | - | 70 | 43 | 64 | 57 | 55 | 31 | 55 | 75 | 64 |
| females | | | | | | | | | | | | |
| Blamah (Bl) | | **87** | | - | 52 | 70 | 73 | 63 | 63 | 63 | 65 | 68 |
| Carolla (C) | | | | | - | 72 | 46 | 43 | 44 | 43 | 61 | 48 |
| Goldilocks (Go) | | | | | **72** | - | 57 | 58 | 44 | 58 | 54 | 60 |
| Grace (G) | | | | | | | - | 62 | 75 | 62 | 65 | **76** |
| Helen (Hl) | | | | | | | | - | 81 | **100** | 61 | 60 |
| Houdina (Hd) | | | | | | | | **81** | - | **81** | 69 | **81** |
| Maria (M) | | | | | | | | **100** | | - | 61 | 60 |
| Popeye (Po) | | | **75** | | | | | | | | - | 72 |
| Samantha (S) | | | | | | | | | **81** | | | - |

Notes

1) Scores represent the % of samples in which each individual was recorded in the same sub-group as each other individual (from the total no. of samples they could have been recorded together.

2) Scores from columns in the top-right of the table are not repeated in the bottom-left of the table unless (3).

3) In each row, the highest score(s) for that individual is (are) highlighted (two if equal).

**TABLE 7. 3** Most frequent travelling companions in 1985 & 1986.

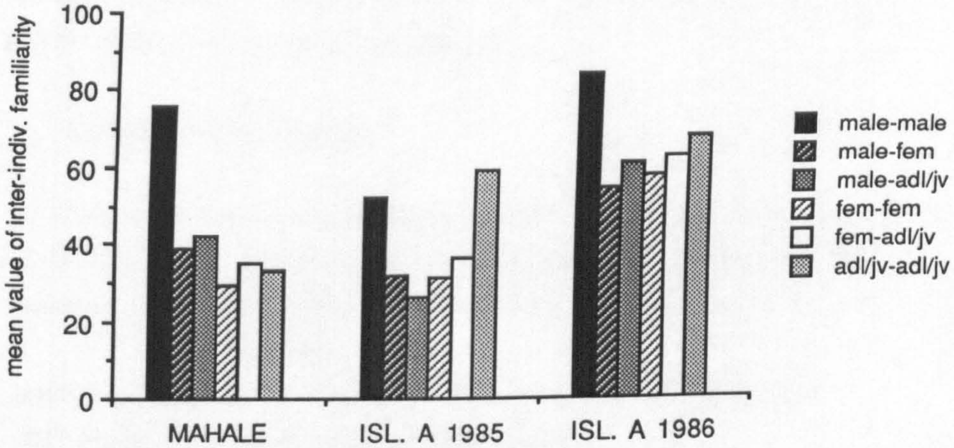
| Subject | Travelling companion 1985 | 1986 | Consistent from 85-86** |
|---|---|---|---|
| males : | | | |
| Daniel | * Sokomodo | - | - |
| Brutus | Sokomodo | * Sokomodo | yes |
| Hermaphrodite | * Goldilocks | - | - |
| Knut | Hermaphrodite | - | - |
| Meryn | * Blamah | * Blamah | yes |
| Sokomodo | * Daniel/ Maki | * Brutus | - |
| females : | | | |
| Blamah | * Meryn | * Meryn | yes |
| Carolla | Popeye | * Goldilocks | no |
| DmW | Maria | - | - |
| Goldilocks | * Hermaphrodite | * Carolla | - |
| Grace | Samantha | Samantha | yes |
| Helen | * Maria | * Maria | yes |
| Houdina | * Popeye | Helen/Maria/ * Samantha | no |
| Maki | Meryn/ Sokomodo | - | - |
| Maria | * Helen | * Helen | yes |
| Popeye | * Houdina | Sokomodo | no |
| Samantha | Houdina | * Houdina | yes |

- = not present

* indicates mutual preference

** excludes pairs which could not remain the same because one member of the pair was not present in 1986

**FIGURE 7.1** Travelling preferences by age/sex class, Mahale and Island A.




adl/jv = adolescent/juvenile (others classes all adult)

Mahale data are from NISHIDA (1968), see text for details on calculation of values.

group is in part due to some of the particularly strong pair bonds mentioned above, which developed in captivity. Perhaps such bonds between adolescents in captivity are more likely to develop in the absence of kinship bonds between juveniles and adolescents with their mother.

NISHIDA'S (1968) second finding, that male-female familiarity is stronger than female-female familiarity in wild chimpanzees, is not found in the study group in 1985 or 1986, where these mean values are similar on both years. GHIGLIERI (1984 :129) found that all classes of female were significantly more likely to travel with other females than with males, which also differs from NISHIDA'S data.

Female chimpanzees seem to form stronger bonds in captivity (De WAAL, 1986; 1989a) than in the wild, where they lead largely solitary lives with their dependent offspring (e.g. NISHIDA, 1968, 1979; GOODALL, 1968). NISHIDA (1968) stated that adult females in the Mahale population interacted infrequently, in contrast to interactions between adult males, or adult males and adult females. Interactions between different age/sex classes will be discussed below.

Mean values of inter-individual familiarity in the study group are higher for all age sex classes in 1986 than 1985, as are overall means for both years (1985 : mean = 39, range = 0-98; 1986 : mean = 62, range = 31-100). This does not seem to be simply a result of decrease in group size (from 16 to 12), but rather an indication of increased group cohesiveness (discussed further below).

Composition of subgroups

Data on the types of subgroups the study group split into are illustrated in Figure 7.2. Definitions of subgroup types referred to in the next section are as follows :

*bisexual group* : adults and subadults of both sexes, but no females with dependent offspring
*unisexual group* : all male or all female group (adults or subadults)
*male group* : two or more adult or subadult males
*female group* : two or more adult or subadult females
*mother group* : adult females with their dependent offspring
*solitary male* : one male only
*solitary female* : one female only

In the study group, the percentage of bisexual groups and all male groups is similar in 1985 and 1986, whereas there is a change in proportion of female groups (which increases) and solitary individuals (which decreases). When compared to data on subgroup composition in wild chimpanzees (Table 7.4), the study group shows similar trends in frequency distribution patterns to wild populations. In 1985, the proportion of lone individuals was high in comparison to wild data, but decreased to a comparable level in 1986. This decrease in solitary travel is another indication of increased group cohesiveness from 1985 to 1986. In 1986, the proportion of unisexual groups on Island A was higher than that for wild populations, which could be due to stronger female-female bonds on the island than in wild populations, but also there were 9 females and only 3 males on the island, increasing the probability of all female groups being recorded.

**FIGURE 7.2** Composition of subgroups, Island A, 1985 & 1986.

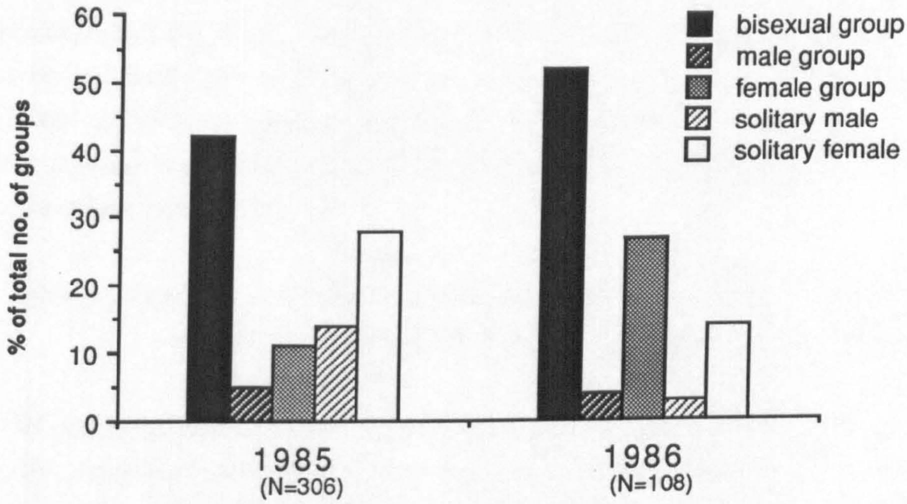



**TABLE 7.4** Composition of subgroups, wild populations and study group.

Scores are a percentage of the total number of subgroups recorded.

| | **Gombe** (N=350) | **Mahale** (N=218) | **Isl.A 1985** (N=306) | **Isl.A 1986** (N=108) |
|---|---|---|---|---|
| mother groups | 24 | 13 | N/A | N/A |
| mixed groups & bisexual groups | 48 | 52 | 42 | 56 |
| unisexual groups | 10 | 11 | 16 | 31 |
| lone individuals | 18 | 21 | 42 | 17 |
| adult groups * | - | 3 | - | - |

N/A - not appropriate (i.e. no mothers with infants on Island A).

* - adult groups are only separated in Mahale data

Note that for the Gombe data, *mixed groups* (males, females, and young) and *bisexual groups* (males, females; but no females with dependent offspring) have been combined to compare with the island data, because no island females had dependent offspring.

Gombe data are from GOODALL (1968), Mahale data are from NISHIDA (1968).

## Size of subgroups

Subgroup size ranged from lone individuals to the entire study group (16 individuals at most at one time). Data on subgroup sizes are illustrated for 4 wild populations and the study group in Figures 7.3 a and 7.3 b. It should be pointed out that data on subgroup sizes from the 4 wild popualtions and the present study group were collected in different ways, either during opportunistic encounters in the forest, at artificial provisioning areas, or at fruiting trees. Details on how data were collected for each study are as follows :

**Gombe** (GOODALL, 1968) : opportunistic encounters in the forest. These data were collected from 1960 -1962, before the chimpanzees were provisioned.
**Mahale** (NISHIDA, 1968) : subgroups arriving at the provisioning area.
**Mt. Asserik** (TUTIN et al., 1983) : opportunistic encounters in forest or savanna.
**Kibale** (GHIGLIERI, 1984) : combination of opportunistic encounters in forest, and observations during vigils spent at fruiting trees.

Data collected from artificial provisioning areas set up by humans may produce a bias towards larger subgroups. WRANGHAM (1975 : 3.60) found that subgroup sizes increased before arrival at the provisioning area in Gombe (see below). This may explain why the Mahale data (NISHIDA, 1968, see Figure 7.3 a) show higher proportions of large subgroups in comparison to data from Gombe (GOODALL, 1968) and Kibale (GHIGLIERI, 1984 : 125).

The higher proportions of large subgroups in Mt. Asserik, Senegal (TUTIN et al., 1983) could be related to differences in habitat type. McGREW et al. (1981) described the habitat of the chimpanzees of Mt. Asserik, and showed that it was more open, i.e. had less woody vegetation, than any other site at which chimpanzees had been studied. This may have affected subgroup sizes at Mt. Asserik. TUTIN et al. (1983) found that larger, mixed subgroups containing adult males were much more common in open, non-forested areas than were solitary individuals or subgroups without males. TUTIN et al. suggested that this could be an adaptation to threat from potential predators when moving in areas with very few or no trees. Four species of potential predators (*Panthera leo, Panthera pardus, Lycaon pictus*, and *Crocuta crocuta*) were relatively common in the area.

**FIGURE 7.3 a** Subgroup size in four wild chimpanzee populations.

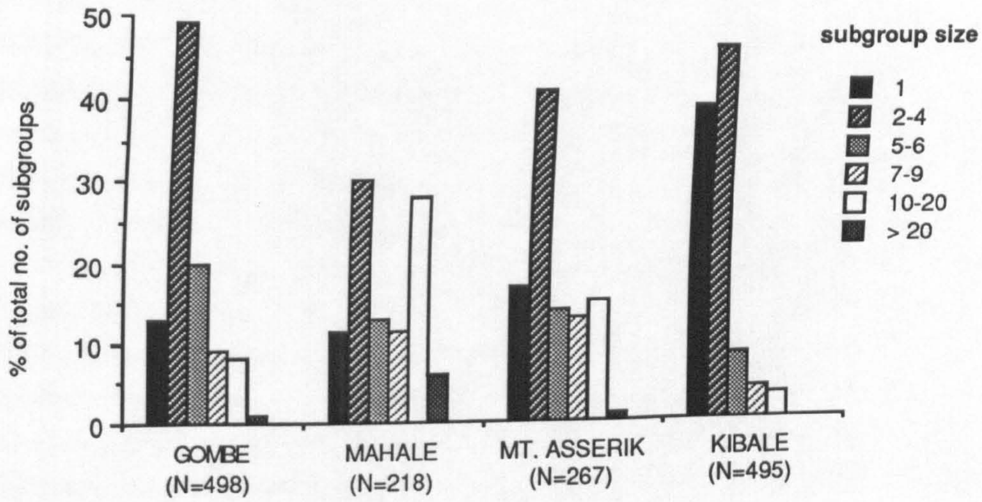
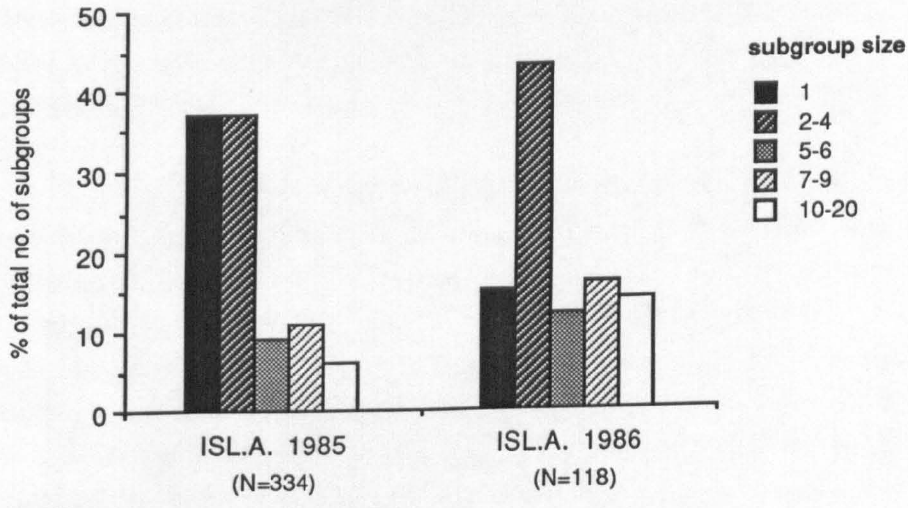



**FIGURE 7.3 b** Subgroup size in study group.




Gombe data are from GOODALL (1968 : 211).
Mahale data are from NISHIDA (1968; adapted from Figure 6, p.180).
Mt. Asserik data are from TUTIN et al. (1983; adapted from Figure 1, p.158).
Kibale data are from GHIGLIERI (1984; adapted from Figure 15, p.125).

Note - data from both NISHIDA (1968) and GHIGLIERI (1984) allow the option of considering a mother with dependent offspring as a solitary unit. Here, however, 'mother' groups are not considered as solitary units.

Some data on subgroup sizes is available from other studies of less habituated populations of wild chimpanzees (REYNOLDS & Reynolds, 1963, 1965; IZAWA & ITANI, 1966; IZAWA, 1970; JONES & SABATER PI, 1971).These data show trends towards larger subgroups than the 4 studies discussed above. Studies of unhabituated populations, however, are biased towards observations of larger subgroups which are more easily located (e.g. by vocalisations). In some of the studies of unhabituated populations (e.g. REYNOLDS & REYNOLDS, 1965; JONES & SABATER PI, 1971), solitary chimpanzees were not observed.

When comparing data from the study group with wild populations, it is interesting to note that the Island A data from 1985 more closely resemble the Kibale (GHIGLIERI, 1984 : 125) data, whereas the Island A data from 1986 more closely resemble data from the other 3 wild populations illustrated in Figure 7.3 a. The main difference between data for the study group between 1985 and 1986 is the decrease in solitary travel. There is also an increase in proportion of larger subgroups. GHIGLIERI (1984 : 123) suggests that the chimpanzees of Gombe travelled in larger than normal parties as a result of provisioning, which lifted the normal constraints of foraging. WRANGHAM (1975 : 3.56) reported that when individual chimpanzees arrived separately at the feeding area in Gombe, they were significantly more likely to leave together when they were fed then when they were not. When WRANGHAM (1975 : 3.60) compared aggregations or party sizes 1 hour before entering the feeding area with 2 hours after leaving, however, there were no significant differences. Provisioning therefore had only a temporary effect on party sizes.

There is a significant difference in subgroup sizes in the study group between 1985 and 1986 ($\chi^2 = 38.04$, d.f. = 4, $p < 0.01$). Provisioning does not account for the difference in sizes of subgroups between 1985 and 1986. In fact the study group was fed fewer days per week in 1986 (mean = 3.4) than in 1985 (mean = 4.5). If provisioning was affecting subgroup size, the opposite trend would have been expected, i.e. subgroups should have been larger in 1985 than in 1986.

A number of field studies of chimpanzees (NISHIDA, 1974; WRANGHAM, 1975; GHIGLIERI, 1984) have suggested seasonal variations in subgroup size, with an increase in size when more food is available. The study group, however, was not observed on Island A during any dry season periods (November-April), when lower water levels meant that chimpanzees on Islands A & C (Figure 2.4) could cross the canal separating them. During these months, the the study group was therefore returned to the laboratory (or in the dry season of 1986/87, half of the group was transferred to another island). It therefore was not possible to test differences in subgroup size in different seasons for the study group.

Solitary travel

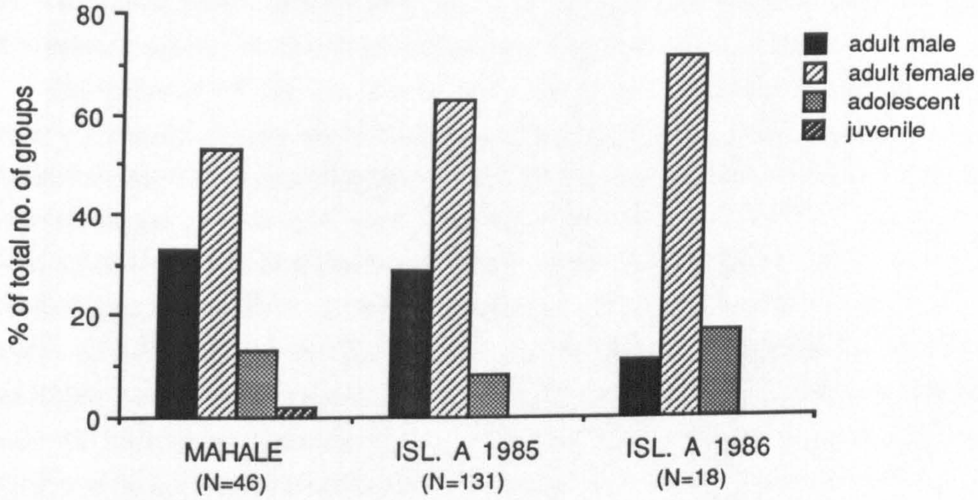
Data on solitary travel for different age/sex classes are illustrated in Figure 7.4. As previously mentioned, records of individuals travelling alone decreased from 1985 to 1986 (42 % to 17%, Table 7.4), but when solitary scores for individuals who were present on both years are compared, the decrease is not significant (Wilcoxon test, $z = -1.78$, $p = 0.074$). The relative proportions of different age/sex classes who travelled alone are similar to those reported by NISHIDA (1968). There is a decrease in proportion of records of adult males travelling alone in 1986, but this is probably due to the fact that there were only 2 adult males on Island A, *Brutus* and *Sokomodo*, and they travelled together more in 1986 (56% of samples in 1985 and 85% in 1986, Tables 7.1 & 7.2). The proportion of adult female and adolescent solitary travel is similar in 1985 and 1986. In the study group and in 2 studies of wild populations where data are given (NISHIDA , 1968; GHIGLIERI, 1984 : 125), females travelled alone more often that males.

There were individual differences in solitary travel in the study group, as was also found by NISHIDA (1968). For example, the adult female Carolla accounted for 45% of adult female solitary score in 1985 and 69% in 1986. In Mahale (NISHIDA, 1968) 1 adult female accounted for 67% of adult female solitary scores.

After release into a semi-free-ranging area, the chimpanzees of the present study who were previously kept in stable groups in enclosures, split into temporary subgroups of different sizes and different individual composition. The types and sizes of subgroups formed showed similar trends to those recorded in wild populations of chimpanzees. Even after many years in captivity, chimpanzees can show natural trends in subgroup formation when given the chance to.

The sizes and composition of subgroups formed were presumably a result of both *social* (in terms of individual choice in travelling companions) and *environmental* (in terms of foraging limitations) factors. The study group was semi-provisioned, and therefore less constrained by foraging limitations on subgroup size than unprovisioned wild populations. When provisioning was decreased (from 1985 to 1896), there was an increase in proportion of larger subgroups. This difference would be explained by social rather than environmental factors, and appeared to indicate an increase in group cohesion from 1985 to 1986.

**FIGURE 7.4** Solitary travel by different age/sex classes, Mahale and study group.




Mahale data are from NISHIDA (1968).

## Aggression

### Studies of aggression in different conditions

Early studies which compared levels of aggression in captive primate groups with free-living conspecifics showed that captive groups exhibit higher levels of aggression than wild groups (e.g. ROWELL, 1969 : baboons; SOUTHWICK, 1969: rhesus monkeys). Studies of captive primates under different conditions then related levels of aggression to available space, suggesting that a decrease in available space led to increased levels of aggression (e.g. SOUTHWICK, 1967 : rhesus monkeys; ELTON & ANDERSON, 1977 : baboons). Recent studies, however, have questioned this simple relationship between aggression levels and available space (NIEWENHUIJSEN & DE WAAL, 1982 : chimpanzees, DE WAAL, 1989b : rhesus macaques).

NIEWENHUIJSEN & DE WAAL (1982), when comparing social behaviour in a group of captive chimpanzees in 2 different enclosures of different area (outdoor summer and indoor winter housing), found that although the frequency of aggression increased in the smaller indoor winter enclosure, it did not increase to the extent found in earlier studies of primates (e.g SOUTHWICK, 1967; ELTON & ANDERSON, 1977). Moreover, frequencies of affiliative behaviour such as submissive greeting and social grooming increased by a greater level than aggressive behaviour. NIEWENHUIJSEN & De WAAL suggested that these increases in affiliative behaviour may have been a means of regulating aggression within the group in the more crowded conditions.

De WAAL (1989b), in a review of the literature on the relation between captive environments and primate social behaviour, in particular aggressive behaviour, concluded that in many earlier studies of aggression following a reduction in available space, there were confounding effects of novelty of the environment. A dramatic change in the physical environment can create a need for social reorganisation, which is likely to involve aggression. Thus, a new environment of a larger area may also produce increased levels of aggression. ROTH & ALEXANDER (1971) reported serious fighting and killing in a group of Japanese macaques (*Macaca fuscata*) following release into a corral 73 times larger than their original enclosure. After a number of years in thecorral, an increase in aggression could again be produced by crowding the group into a smaller pen. ROTH & ALEXANDER concluded that removal from a familiar habitat was adequate to provoke mobbing, independent of the characteristics of the new habitat.

De WAAL (1989b) suggested that more instructive comparisons of the relationship between available space and aggressive behaviour could be made by comparing groups of the same species which had lived under different conditions for many years. Such data are not available for chimpnzees, but De WAAL (1989b) made such a comparison between rhesus monkeys (*Macaca mulatta*) in different established groups in the wild (TEAS et al, 1982), in a large corral (BERNSTEIN et al, 1983), and in a smaller cage (De WAAL & LUTTRELL, 1986). When De WAAL compared the rates of aggression in the 3 groups, the data contradicted the idea of a clear correlation between amount of available space and aggressive behaviour. The rate of aggression by males showed considerable variation, but was lowest in the corral, and highest in the free-ranging group. De WAAL suggested the absence of male migration in captive groups may have been responsible for the comparatively low aggression levels in the males.

There is therefore not such a simple relationship between available space and aggression as early studies suggested. Different factors play a role, such as familiarity of group members, familiarity of the environment, and also inter-species differences in grouping patterns and in response to increased population densities, in terms of effectiveness of conflict management. Unlike most New World and Old World monkeys, chimpanzees do not travel in constant groups in the wild, and it is unlikely that all members of a chimpanzee community are ever all together at one time. It is therefore not surprising that problems with aggression between group members have been encountered in attempting to keep large numbers of chimpanzees together in captivity (e.g. WILSON & WILSON, 1968). These problems can be overcome, however, with better design of enclosures, and separation of chimpanzees at feeding times (e.g. Van HOOFF, 1973a).

Differences in aggression levels in the study group before and after release are discussed below.

Rates of aggression before and after release

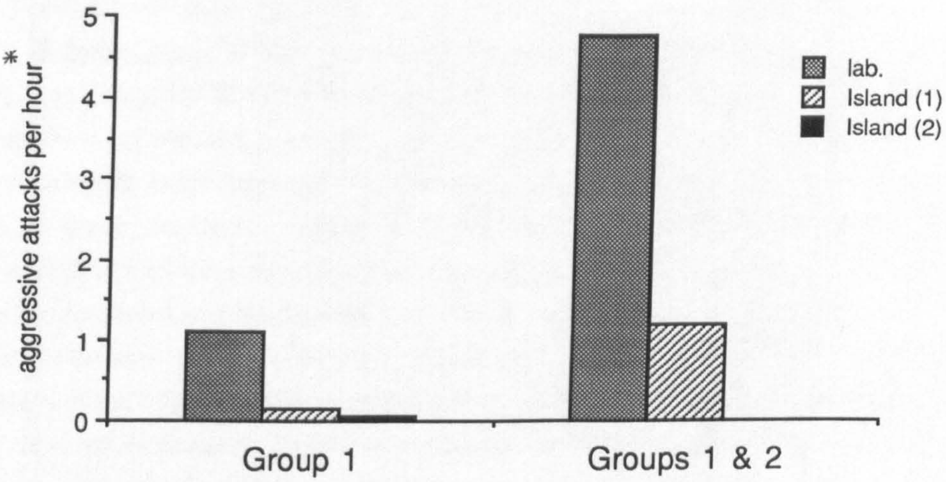
Rates of aggression before and after release in Group 1 and in Groups 1 & 2 together are illustrated in Figure 7.5. For both Group 1 and Groups 1 & 2 together, the rate of aggression following release dropped dramatically from that at the laboratory. The rate of aggression when Groups 1 & 2 were combined at the laboratory (excluding aggression on the first day of introduction) was almost five times the rate for Group 1, but decreased following release. Familiarity of group members and housing conditions therefore may both have affected rates of aggressive encounters.

Events preceding aggression

Data on the events which preceded aggression are illustrated in Figure 7.6. Each of the situations which preceded aggression will be discussed below.

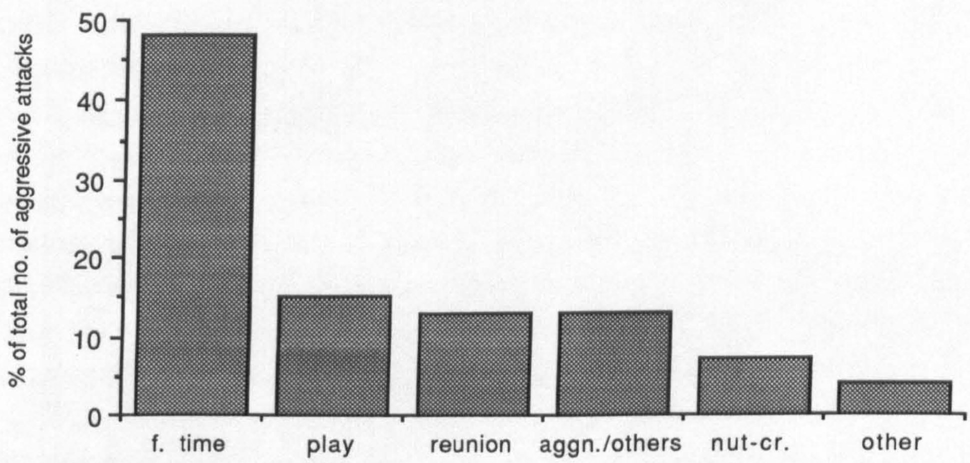
1) Feeding time : A large proportion (48%) of aggressive attacks occurred during feeding time on Island A. Feeding time also produced higher rates of aggression at the laboratory (Figure 3.22). WILSON & WILSON (1968) reported a high frequency of aggression preceding and during feeding in a group of captive chimpanzees in a large outdoor enclosure. In the wild, chimpanzees normally forage in small subgroups or alone. Setting up a feeding station in the forest at Gombe, however, produced larger aggregations of chimpanzees (WRANGHAM, 1974). When WRANGHAM compared aggregation sizes and aggression levels of feeding days and non-feeding days at the feeding area, he found that aggregation sizes were significantly smaller on non-feeding days, and that there were significantly more aggressive attacks on feeding days (mean = 5.1 per day) than on non-feeding days (mean = 0.2 per day). WRANGHAM suggested that feeding probably increased attack frequencies both by eliciting more attacks within a given aggregation size and by promoting large aggregations. BYGOTT (1979) also found

FIGURE 7.5 Aggression at laboratory and on Island A.




* for good observation hours (i.e. majority of group in sight)
Island (1) = first island study period for group in question.
Island (2) = second island study period for Group 1.

FIGURE 7.6 Events preceding aggression on Island A.




f.time = feeding time; play = social play;
reunion = meeting between individuals who have been separated;
aggn./others = aggression between others;
nut-cr. = nut-cracking ; other = unknown or unusual context

that the frequency of attacks increased with group size away from the feeding area (median group size with attacks = 9; overall median group size = 3).

The study group, however, was only observed on feeding days, therefore it was not possible to measure aggression levels on the island on non-feeding days.

2) Social play : Fifteen per cent of aggressive attacks occurred following social play interactions. De WAAL (1980) reported that social play preceded 13 % of aggressive interactions (of which the preceding event was known). On the island, aggression could spontaneously erupt between 2 individuals play-wrestling, presumably when play became too rough. On other occasions, a third party was involved either with or without the knowledge of the individuals playing. For example, the adolescent female *Maria* approached *Helen* and *Meryn* who were playing, and pinched *Meryn*. *Meryn* seemed to think *Helen* had done this, because he screamed and bit *Helen*, which started a fight between them. *Maria* then supported *Helen* in the fight and together they chased *Meryn* away. On other occasions, a third individual directly intervened in playful interactions by pulling on or biting one of the pair playing.

3) Reunion : When the subgroups of chimpanzees who had been travelling separately on Island A met at the feeding site, this occasionally resulted in aggressive interactions. It should be pointed out, however, that this was also when the chimpanzees were waiting to be fed, which may have produced tension which led to aggression. BAUER (1974) found that the most frequent context of aggressive attacks in wild chimpanzees was at a reunion. The level of excitement on arriving at the feeding site therefore probably accounted for some of these attacks, irrespective of tension increasing before feeding time.

4) Aggression between others : Thirteen percent of aggressive attacks led to other attacks. these were either supportive attacks, which involved a third individual intervening on behalf of one of a pair of individuals (see below), or were attacks involving different individuals but which occurred during or immediately after another aggressive interaction in the group and which therefore seemed to be related to the first. For example, if one group member began to display during a fight between 2 others, and then attacked an individual apparently uninvolved with the interaction.

Recent occurrence of other attacks often produced more aggression both in wild chimpanzees (BYGOTT, 1974; GOODALL, 1986 : 319), and in captive chimpanzees (De WAAL, 1980). De WAAL stated that despite the ample size of their enclosure, the main source of aggression in the Arnhem chimpanzee group was aggression between others.

5) Nut-cracking : Seven percent of aggressive interactions occurred in the context of nut-cracking, and were related either to attempted stealing of nuts, or limited access to

stones. Examples of aggression at nut-cracking sites are given in the previous chapter.

6) Other : The final category 'other' includes either aggressive incidents in which the context was not clear, or unusual events which produced aggression in others, such as anaesthetising one group member for removal from the island (due to illness).

## Aggression and support between sexes

Data on aggression between different age/sex classes on Island A are illustrated in Figure 7.7, and are summarised by sex in Figure 7.8. Most aggression was shown between adult males and females, and least between males. The 3 adult males were released onto the island last, and perhaps because of this they were no longer dominant over the females of the group as they had been at the laboratory. The females of the group combined forces and could, for example, chase away an adult male during aggressive encounters, a situation which was not observed at the laboratory. Aggression by adult female chimpanzees towards adult males was not recorded in any of 541 aggressive encounters between wild chimpanzees (GOODALL, 1986 : 365), but occurs in captive chimpanzee groups. Following the introduction of the 3 adult males to the Arnhem chimpanzee group over one year after the females had been introduced (ADANG et al., 1987), the females dominated these males until the two top-ranking females were temporarily removed. During this temporary removal, the 3 males succeeded in attaining the highest ranks, and were able to maintain these positions after the reintroduction of the 2 females (De WAAL, 1978).

In the study group, the adult males began to support one another in aggressive encounters with females one month after the males were released. De WAAL (1978 : 273) defined a supporter as

*"the initiator of a new 'agonistic dyad' with one (and only one) of the individuals who were already involved in an 'agonistic dyad'. The new 'agonistic dyad should start during the initial dyad or just after its ending (i.e. within 30 seconds)."*

An 'agonistic dyad' (De WAAL, 1978) is a dyadic interaction between individuals which can be considered to be of an agonistic nature, based on Van HOOFF'S (1974) analysis.

Of the 3 adult males, only *Sokomodo* supported another male during agonistic interactions, and he always supported *Brutus*. At the laboratory these were the second and third ranking males respectively, but on the island they appeared to have equal rank. *Sokomodo* may have been supporting *Brutus* in an attempt to improve his status, as has described for adult male interactions in both captive chimpanzees (De WAAL, 1984), and

FIGURE 7.7 Aggression between different age/sex classes, Island A.

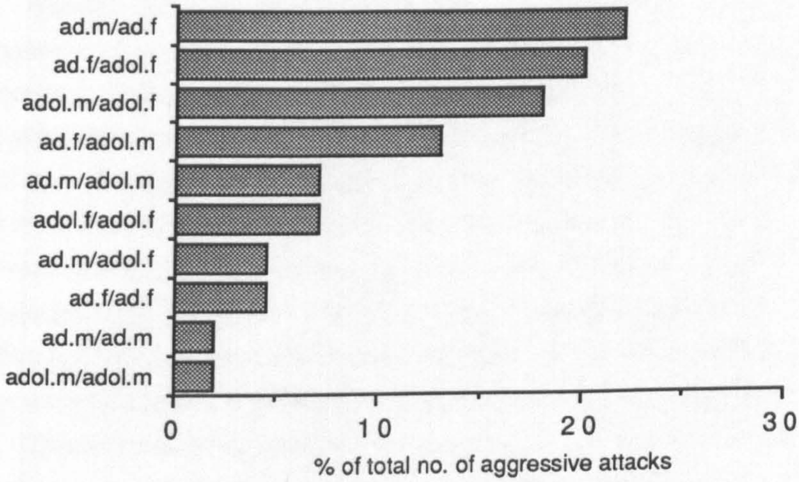
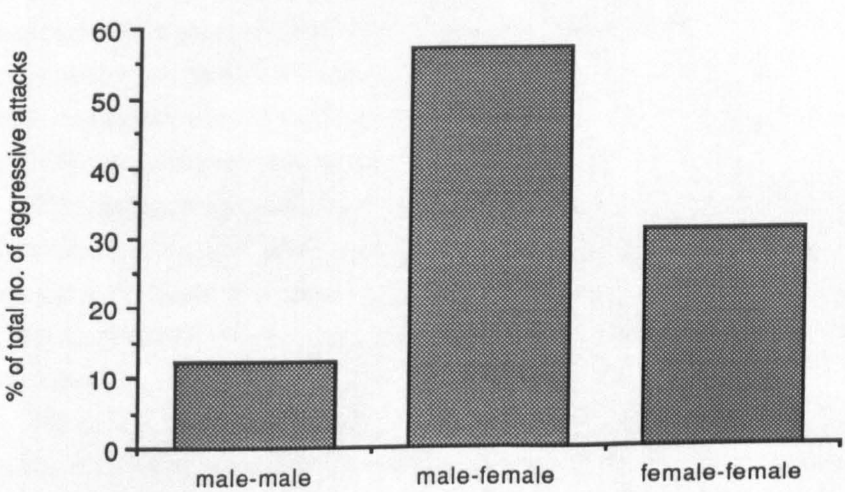



FIGURE 7.8 Aggression between sexes, Island A.



wild chimpanzees (NISHIDA, 1983). Despite the fact that *Sokomodo* supported *Brutus* in agonistic interactions with females, and that the males frequently travelled together (discussed above) they did not, however, manage to attain the top-ranking status that they had held at the laboratory.

*Daniel*, the alpha male of the study group, appeared to have less influence on aggressive interactions of other group members on the island in comparison with the laboratory. This may have been a reason for the high level of aggression between adult and adolescent females.The majority (67%) of these aggressive encounters were at feeding time, when the adult female *Samantha* attacked lower-ranking adolescent females and took food from them. At the laboratory, if there were any aggressive incidents between other group members, the alpha male of the group usually intervened (by charging towards the pair involved in a fight), which split up the fight and stopped aggression from proceeding further. On Island A, however, Daniel seemed to ignore aggressive encounters between other group members, and these continued.

Overall rates of aggression between sexes are illustrated in Figure 7.8. Inter-male aggression occurred least frequently, but when numbers of each sex are taken into account, the differences in frequencies of aggression between sexes are not significant ($\chi^2 = 1.8$, 2 degrees of freedom, $p > 0.05$).

When comparing support from others during aggressive encounters (Figures 7.9 & 7.10), adolescent females showed more support of others than any other age/sex class. Many of these (55%) supportive interventions of adolescent females were on behalf of their preferred travelling companions (as listed in Table 7.3). De WAAL (1978, 1984) reported that in a group of captive chimpanzees, female support was often an expression of familiarity which did not aim at future reward, for example, protection of friends, whereas males were more inclined to use opportunities for bond formation if these might be of help to maintain a certain rank.

The next most frequent form of support in the study group (Figure 7.9) was adult male support of another adult male (in all cases *Sokomodo* supporting *Brutus*). Adult males did not support any other age/sex class. These data are therefore in agreement with De WAAL'S (1978, 1984) findings on sex differences in support strategies in captive chimpanzees.

When support data are split into male and female data (Figure 7.10), the most frequent class of support is females supporting other females. This is in contrast to wild female chimpanzees, who virtually never support one another, other than a report by

FIGURE 7.9 Support by different age/sex classes during aggressive encounters.

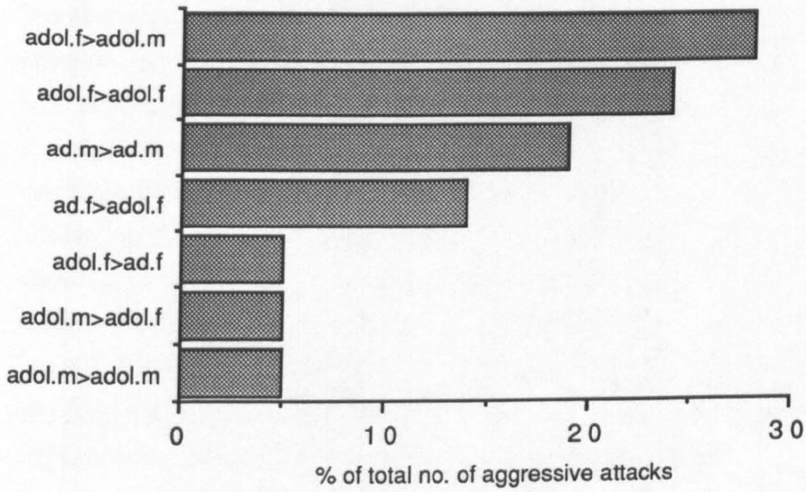
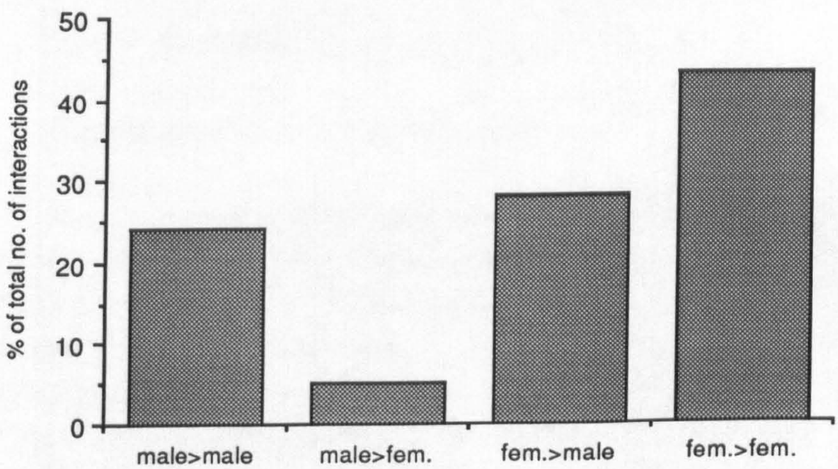



FIGURE 7.10 Support by different sexes during aggressive encounters.



BYGOTT (1974 : 118) that two or more adult females sometimes combined forces to chase or even attack young adult males displaying at them. Differences in female chimpanzees' behaviour in the wild and in captivity are discussed by De WAAL (1989b). When comparing hierarchies, coalitions, reconciliations, and social bonding between wild and captive chimpanzees, De WAAL found that captive females differed from wild females in social bonding and coalition (or support) formation, and that in both types of environment they had less formalised hierarchies than males, and showed significantly less reconciliatory behaviour than males. GOODALL (1986 : 365) also stated that reconciliation was less likely to occur between adult females after aggression when comparing male-male with female-female aggression. De WAAL (1989b : 255) concluded that "female chimpanzees lost or did not evolve the mechanisms of social dominance comparable to those of their male conspecifics", which he related to their relatively solitary life style in natural conditions, which suits their foraging needs (e.g. see WRANGHAM & SMUTS, 1980). Female chimpanzees therefore only show social bonding when competition for food is reduced in captive environments, whereas male chimpanzees show bonding both in captivity and in the wild.

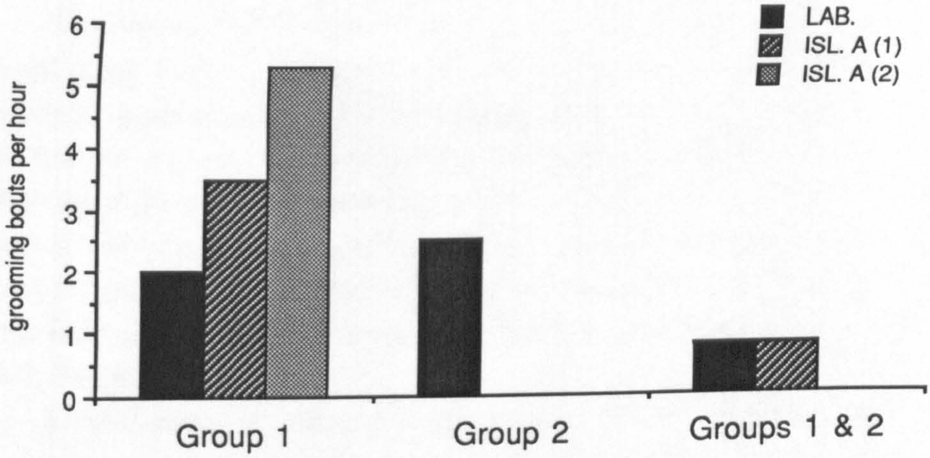
It would be interesting to see if female chimpanzees released from captivity into a free-ranging area where they were not provisioned would maintain bonds which had developed in captivity, or if social bonds between females would more closely resemble those of wild chimpanzee females. That is, under different foraging constraints, would the females be less likely to associate together ? In the present study, where the group can be considered as semi-provisioned, female bonding remained strong.

## Social Grooming

### Rates of grooming before and after release

Data on grooming rates before and after release are illustrated in Figure 7.11. Grooming bouts per hour are compared between laboratory and island data. A grooming bout is defined here as a continuous grooming interaction, not separated by more than 2 minutes, between a pair of individuals. At the laboratory, data were available on lengths of grooming bouts (to the nearest minute), whereas on the island the beginning and end of grooming bouts were not always so accurately recorded. Therefore, number of grooming bouts per observation hour, regardless of their length, are compared between the island and laboratory data.

**FIGURE 7.11** Social grooming at the laboratory and on Island A.




ISL. A (1) = first island study period for Group 1 or Group 2.
ISL. A (2) = second island study period for Group 1.

For Group 1 (Figure 7.11), grooming rates increased following release onto Island A. CLARKE et al. (1982) found that grooming rates increased in a group of 4 laboratory chimpanzees released onto a small (0.05 ha) island in the United States, although it was still "characteristically rare". NIEWENHUIJSEN & De WAAL (1982), found that a decrease in available space (following transfer from the summer to winter enclosure) produced a significant increase in grooming frequency in the Arnhem Zoo chimpanzee group. They suggested that grooming may have served to regulate tensions more in the crowded situation. NIEWENHUIJSEN & De WAAL'S data also suggested an overall increase in grooming frequencies over the years. This trend is apparent for Group 1, which shows a further increase in their first (1985) to their second (1986) island study period.

Rates of grooming in Groups 1 and Group 2 at the laboratory were similar. When both groups were introduced, however, grooming rates dropped and did not increase following release. It should be noted, however, that these data are taken from only 1 week before release and 1 month after release for Groups 1 and 2 combined (whereas all other data sets come from at least 3 months of observation), and were therefore collected during a period of group instability.

## Context of social grooming on island

The majority (73%) of grooming bouts were recorded following the chimpanzees arrival at the feeding area of the island and before they were fed. This tendency to participate in social grooming following arrival at the feeding area could be related to the fact that the chimpanzees were meeting after a period of separation. BAUER (1975, 1979) found an increase in grooming rate of travelling focal chimpanzees following reunion, and suggested that a reward for joining a party was the greater possibility of increased grooming. Early laboratory evidence also suggests that grooming frequencies increase on meeting after a period of separation in captive chimpanzees (CRAWFORD, 1942; FALK, 1958).

Another possible explanation for the increased likelihood of grooming at the feeding area could be the fact that provisioning occurred there, and that there was tension between group members before provisioning. At the laboratory, there was an increase in grooming frequency before feeding time (Figure 3.30).

The fact that grooming rates were higher on the island than at the laboratory for Group 1 suggests that on the island grooming levels were more related to maintaining social bonds (following separation which could only occur on the island) than to tension reduction (which would be expected to be more important in a crowded than semi-free-ranging situation). The fact that individuals were more likely to groom other individuals who had been travelling in separate subgroups (71 % of grooming bouts in 1985, although this dropped to 57 % in 1986) also supports the theory that grooming on arrival at the feeding area was related to maintaining social bonds. BAUER (1979) also found that following reunions between wild chimpanzees, individuals were more likely to groom others who had been travelling in a different subgroup.

Overall, therefore, the increase in grooming frequency observed in Group 1 following release was apparently more related to maintaining social bonds following periods of separation than to tension reduction. If tension reduction had been a more important factor, higher frequencies of grooming would have been expected when Groups 1 and 2 were together, but this was not found.

## Social Play

Following release, chimpanzees often played in the interior of the island (Figure 7.12), particularly at the "rest spot" (see below), but never at the feeding area. Frequencies of social play at the laboratory and on Island A are illustrated in Figure 7.13. For Group 1 and Groups 1 & 2 together, the overall frequency of social play decreased following release onto the island. NIEWENHUIJSEN & De WAAL (1982), found that the frequency of social play in the Arnhem Zoo chimpanzee group was significantly lower in their smaller winter enclosure than in their summer enclosure. When data from the study group are split into age/sex class (Figure 7.14), however, it can be seen that the adolescent females and the juvenile male accounted for the majority of play interactions on the island, and that adult males and females and adolescent males accounted for the decrease in frequency of social play on the island. In the wild (GOODALL, 1968 : 260; 1986 :370) the frequency of play behaviour shown by chimpanzees decreases with age. Perhaps in captivity, adult chimpanzees show higher frequencies social play because of limited other pastimes or because of increased time spent together with other individuals, including younger group members. Following release into a free-ranging site, however, the frequency of social play by adults in the group decreased.

All social play that was observed on the island occurred in the interior of the island, and never at the feeding area. Most (85 %) social play interactions occurred at an area in the interior of the island that came to be called the "rest spot". In the first weeks of release when walking in the interior of the island, the author always stopped in this area which had a clearing and therefore better visibility than other areas in the interior of the island. This area then became used by the chimpanzees for sitting or lying around, foraging, grooming, or playing, and the chimpanzees stopped there of their own accord when they were ahead of the author. The chimpanzees seemed to be more "relaxed" in this area than in the feeding site, and this may have been the reason for increased likelihood of social play in this area. This can perhaps be related to the increase in social play at the laboratory after 16.00 hours when the laboratory staff left and after which the chimpanzees seemed more relaxed and aggression levels were low (Figure 3.30).

**FIGURE 7.12** Helen and Meryn play wrestling on Island A.

FIGURE 7.13 Social play at laboratory and on Island A.

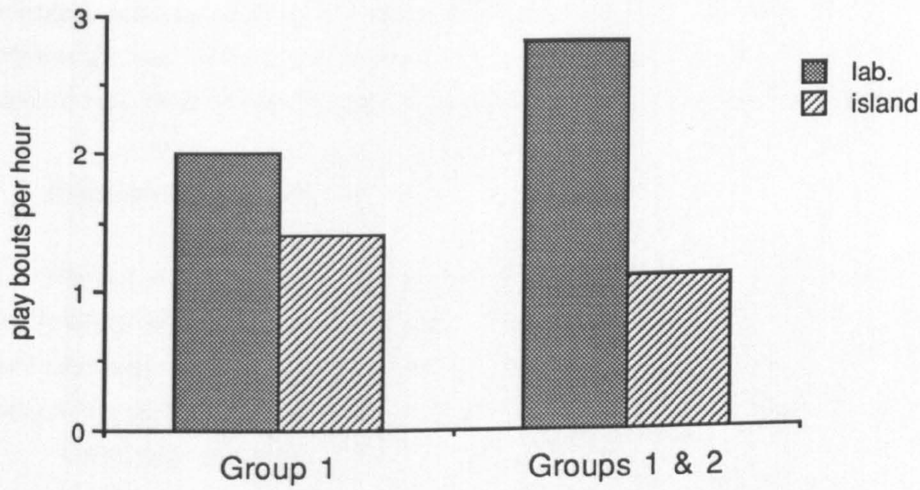
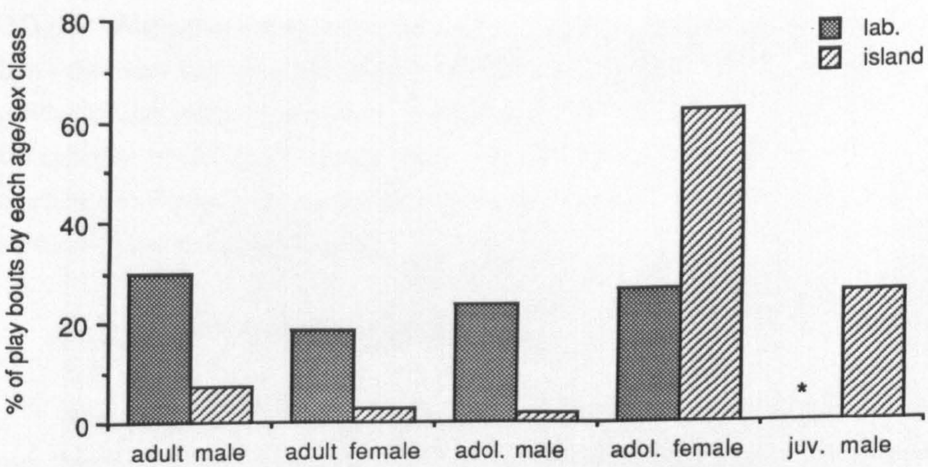



FIGURE 7.14 Social play by different age/sex classes.




Data are from Group 1 only, because composition of Group 2 was more variable.

* The juvenile male Meryn was added to Group 1 shortly before release, therefore his contribution to overall play data is limited to island data only in this figure.

## Sexual Behaviour

During a 3-month study of Group 1 at the laboratory, 24 copulations were recorded, whereas during 3 months of island study, 53 copulations were recorded. Laboratory and island copulations were not converted into rates per hour, however, because they were infrequent events, and only occurred when females had swellings.

### Interference of copulations

During copulations by adults on Island A, sub-adult group members often interfered in copulations by rushinfg towards the copulating pair, jumping around them pant-grunting, and sometimes touching or hitting the copulating pair (Figure 7.15). Interference of copulations by wild chimpanzees has been discussed by TUTIN (1979a).

Only one group at the laboratory (Group 1b) contained both adults and adolescents, and the male involved in the 7 copulations recorded for this group was the adolescent male *Hermaphrodite*. No other adolescents in the group interfered in these copulations. On the island, however, where all members of Group 1 were together, other group members interfered in 75 % of copulations recorded. The proportion of copulations interfered with by each age/sex class are illustrated in Figure 7.16. Adolescent and juvenile males interfered in more copulations than adolescent females. TUTIN (1979a) also found that in the wild immature males interfered in more copulations than immature females, and that males interfered in copulations of both related and unrelated individuals, whereas females only interfered in copulations of related individuals. In the study group there were no related individuals, however, female interference of copulations may be understood when the sex differences in interference are taken into account, as below.

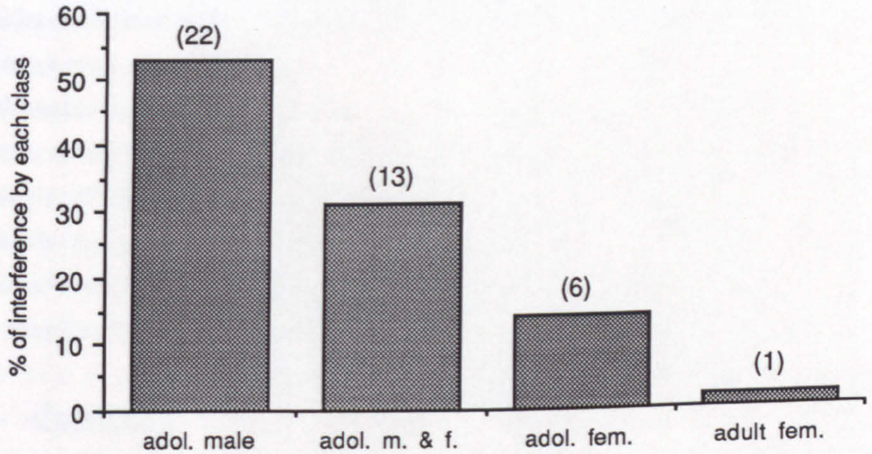
### Sex differences in interference behaviour

When adolescent males interfered in copulations, they rushed to the copulating pair, directing their attention to the adult male, pant grunting and bobbing around him, and sometimes touching or hitting him. Adolescent females on the other hand approached silently, crouched in the same position as the female of the pair, and attempted to push themselves between the copulating pair. One adolescent female, *Blamah*, rather than

FIGURE 7.15 Interference of a copulation on Island A.

Adult male Sokomodo copulating with Popeye (head visible) on arrival at feeding area. Three subadult group members are interfering.

**FIGURE 7.16** Interference of copulations by other group members.




(N)

adol.male = adolescent (or juvenile) male(s) only interfering
adol. m. & f. = adolescent male(s) and female(s) interfering at same time
adol fem. = adolescent female(s) only interfering
adult fem. = adult female interfering (with subadult males and females)

trying to push herself between the copulating pair, went behind the male and pressed her genital area against the males rear end. NISHIDA (1979) described sex differences in interference behaviour of wild adult chimpanzees. High-ranking males interrupted matings of subordinate males by charging and hitting the male (also described by TUTIN, 1979a), and estrous females forced themselves into the mating pair and pushed aside subordinate females and pressed their genital area to the male's penis. The types of interference shown by adolescents on the island may therefore have been early signs of the development of adult patterns of interference as described by NISHIDA (1979). TUTIN (1979a) suggested one possible explanation for adolescent males' interference of copulations was that it was a precocious form of possessiveness, and that their behaviour could be based on the same motivational system as adult males attempting to monopolise receptive females.

Responses to interference

The two adult males, *Sokomodo* and *Brutus* (*Daniel* was not observed copulating on the island, see Appendix 7.1) reacted differently to interference. *Brutus* often hit the adolescents interfering when he copulated, whereas *Sokomodo* seemed to ignore them. *Brutus* was also seen 3 times hitting younger group members who interfered when *Sokomodo* was copulating, in an apparent attempt to keep them away from *Sokomodo*. Once, when *Meryn* was rushing towards *Sokomodo* who was copulating, *Brutus* hit *Meryn*, throwing him onto his back. This could either have been for *Sokomodo's* benefit, by stopping *Meryn* from interfering when *Sokomodo* was copulating, or for *Brutus'* own benefit, since he often copulated with the same female after *Sokomodo*, and he may therefore have been trying to keep *Meryn* away before he began copulating.

Consortship

Consort behaviour in wild chimpanzees, as described by McGINNIS (1979) and TUTIN & McGINNIS (1981) involves a male and a receptive female, plus any dependent offspring of the female, travelling together, ceasing all loud vocalisations, and avoiding encounters with other chimpanzees. The consort pair often moves to the edge or even outside the normal community range.

On Island A, what can be called a 'consort trio' rather than pair was observed in October 1985. From their release in June 1985 until the release of the adult males in August 1985, the adolescent males *Hermaphrodite* and *Knut* copulated with females when all group members were present. Following the release of the adult males, however, they were only seen copulating when the adult males were not present. HAYAKI (1985) found that in wild chimpanzees, the presence of adult males was enough to prevent adolescent males from copulating.

In October 1985, when *Goldilocks* had a swelling, *Hermaphrodite* copulated with her at the feeding area before the adult males arrived. *Knut* approached and groomed *Hermaphrodite* (which was different from his reaction to adult males copulating). When the adult male *Brutus* arrived and copulated with *Goldilocks*, both *Knut* and *Hermaphrodite* interfered. The same situation occurred 3 days later, then 6 days later *Goldilocks*, *Hermaphrodite*, and *Knut* did not arrive at the feeding site. These 3 chimpanzees often travelled together (see Table 7.1), but at other times had always come to the feeding area. They were found on Island B (using telemetry equipment), and were given food. While eating, *Hermaphrodite* copulated with *Goldilocks* 3 times, and each time *Knut* kissed *Hermaphrodite*. These 3 chimpanzees were not looked for again since it was assumed they were trying to avoid other group members and would return when they chose to. Ten days after they went to Island B, *Knut* came to Island A feeding area again, and 3 days later *Goldilocks* and *Hermaphrodite* also returned to Island A.

During the author's absence in January 1986, John Zeonyuway reported the following incident.*Goldilocks* and *Hermaphrodite* (together with the adult female *Grace*) again travelled to Island B in, when *Goldilocks* had a swelling. Five days after travelling to Island B, they then travelled to Island C (by crossing the canal which was shallow at that time), which was inhabited by a group of 15 chimpanzees released in 1983. *Goldilocks* and *Grace* were unharmed and were returned to Island A, but *Hermaphrodite* (who was wearing a radio-transmitter collar) was found dead on Island C with multiple wounds, presumably having been attacked by the Island C chimpanzees. This can be compared to the risk wild male chimpanzees take by increasing chances of intercommunity encounters when forming a consort pair and moving to the edge, or even outside of the normal range of the community, as discussed by TUTIN (1989b).

No consort behaviour of this kind was observed when the study group was returned to Island A in 1986 (when *Knut* and *Hermaphrodite* were no longer in the group).

<u>Births on Island A</u>

On August 7 1985, almost 3 weeks after her release, *Samantha* gave birth to an infant (her second) on Island A. *Samantha's* first infant, who was born at the laboratory, was removed after 6 weeks because *Samantha* was mistreating him (HANNAH & BROTMAN, in press) by pulling his hair out, poking him with pointed objects, and not handling him correctly. On the Island, *Samantha* handled her second infant properly, but still pulled the infants hair out, a grooming abnormality also seen in her grooming of adult chimpanzees. Ten weeks after *Samantha's* infant was born on the island, *Samantha* seemed to have a poor appetite and was returned to the laboratory. As soon as she was returned to the laboratory, *Samantha's* care of her infant rapidly deteriorated, and she no longer carried the infant, who was then removed. *Samantha* was returned to the island 2 weeks later, and her infant remained at the laboratory.

In September 1986, Grace gave birth on Island A. Grace had successfully reared previous infants (HANNAH & BROTMAN, in press), but was returned to the laboratory with her infant both because she had a suspected prolapse, and because *Samantha* had taken her infant from her. *Samantha* was anaesthetised for retrieval of the infant. *Grace* and her infant remained at the laboratory until her infant died from pneumonia at 3 months old.

*Houdina* was pregnant, but prematurely aborted in August 1986. These were the only pregnancies and births recorded on the island during the study period. Samantha was later suspected of killing 2 infants on the island (BROTMAN, pers. comm.), so she was returned to the laboratory.

In February 1989 (pers. obs.), 5 of the island females were successfully rearing their infants on a smaller island they had been transferred to, and 1 female was pregnant.

## STEREOTYPED OR ABNORMAL BEHAVIOUR AFTER RELEASE

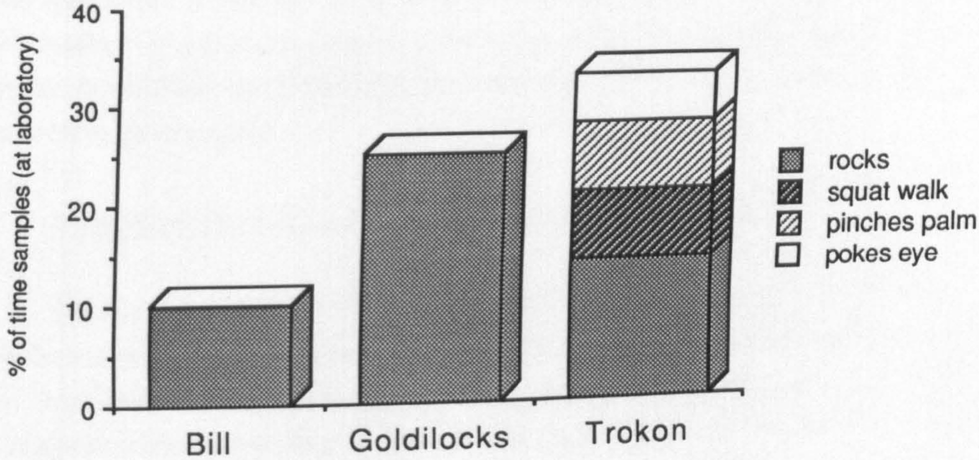
Of the 11 subjects of Groups 1 & 2 who showed stereotyped or abnormal behaviour (e.g. see WALSH et al., 1982) at the laboratory (Table 3.1), 9 were also studied after release onto Island A. These 9 subjects can be split into those whose stereotyped behaviour changed following release, and those whose behaviour remained the same.

### Decrease in stereotyped behaviour after release

All 3 of the subjects who showed stereotyped rocking behaviour before release (Figure 7.17) stopped this behaviour following release. *Bill* was seen rocking while he was inside the cage at the shore of the island before his release, and was once seen going inside the cage and rocking 2 days after release, but thereafter he was not seen rocking again. *Goldilocks* and *Trokon* were not seen rocking at all following their transfer from the laboratory, nor was *Trokon* seen showing any of the other 3 stereotyped behaviours he showed at the laboratory. This was a dramatic change for 3 subjects who were recorded showing stereotyped behaviour on 10-33 % of samples at the laboratory.

CLARKE et. al. (1982) reported a dramatic decrease in stereotyped behaviour of 3 laboratory chimpanzees released onto a small (0.05 ha) island in the United States. The frequency of stereotyped behaviour rapidly diminished then became intermittent following transfer to the island for the subject who had previously shown the highest frequency of stereotyped behaviour (waving his finger in front of his face). A subject who had rocked frequently at the laboratory was never seen rocking on the island, and another who had shown a low level of rocking was only once seen rocking following transfer onto the island.

**FIGURE 7.17** Stereotyped behaviour of Bill, Goldilocks, and Trokon.




See Table 3.1 for definitions.

In PFEIFFER & KOEBNER'S (1978) study, both an increase in group size and release onto a small (0.13 ha) island affected rates of stereotyped behaviour. Two months after introduction to 6 other chimpanzees at the laboratory, 2 chimpanzees who had previously been kept alone and who had shown multiple stereotyped behaviour patterns, showed a reduction in stereotypies. Two other subjects who had been kept in a smaller group before showed an increase in stereotyped behaviour when the group size was increased at the laboratory. Following release onto an island, however, the rates of stereotyped behaviour shown by these 2 subjects dropped to less than a third of the rate at the laboratory.

When *Trokon* was returned to the laboratory 3 weeks after release because he was ill, he resumed his previous stereotyped behaviour. When *Goldilocks* was returned to the laboratory in the dry season of 1985/86, she also resumed rocking, but not to the same extent as before (17 % of samples compared to 25 % of samples before release).

The fourth subject to show a change in abnormal behaviour following release was *Brutus*. At the laboratory, *Brutus* was recorded self-grooming on 9 % of samples, which was the highest self-grooming rate recorded. While grooming, *Brutus* pulled hair from the underside of his forearms, until they were bald. Although his self-grooming frequency was not systematically recorded following release onto Island A, he apparently did not groom himself so frequently, or did not pull his hair out when he was grooming, because the hair in his forearms grew in again. NIEWENHUIJSEN & DE WAAL (1982) also found that at Arnhem Zoo, when the chimpanzees were in their smaller winter enclosure, they pulled out their own hair and most had bald patches by the end of each winter, but the hair grew in again very soon after they were allowed into their larger summer enclosure again.

Stereotyped/abnormal behaviour which continued after release

Two subjects who showed very situation-specific abnormal behaviour at the laboratory continued to do so following release. These subjects were *DmW*, who rocked her head when holding her hand out for food, and *Sokomodo*, who made raspberry vocalisations when grooming. *Sokomodo* also clapped his hands when inviting females to copulate. Hand-clapping is included in WALSH et al.s (1982) ethogram of stereotyped and abnormal beehaviours. In the context *Sokomodo* clapped his hands, however, this could be considered a useful signal, even if different from signals used by wild male chimpanzees (e.g. NISHIDA, 1980).

*Carolla*, who sucked her big toe at the laboratory, continued to do so after release, but only when waiting at the feeding site before feeding time. *Sokomodo*, who had only been kept in the same enclosure as *Carolla* shortly before release, and who had not been seen sucking his toe before, was occasionally seen sitting near *Carolla* (when she was sucking her toe), sucking his toe. When he was returned to the laboratory for a temporary stay (and when he was also housed together with *Carolla*) this behaviour appeared to increase in frequency.

*Samantha*, who pulled hair from herself and other chimpanzees while grooming, continued this behaviour following release, and also tried to do the same to human observers. Other group members tolerated this behaviour, and it did not occur frequently enough for them to show any loss of hair. When *Samantha's* baby was born on the island, however, the baby was almost completely bald all over within a few days of birth (HANNAH & BROTMAN, in press).

*Wolfram*, who showed a stereotyped behaviour which resembled a suckling response (by putting his tongue between his lower and upper incisors, then moving his jaw gently up and down), showed this behaviour both before and after release.

It is interesting to note that the behaviours which to the observer seem more 'disturbed' such as eye poking, and stereotypic rocking, all ceased after release, whereas other forms of stereotypic or abnormal behaviour continued. Stereotypic rocking (at continual levels rather than the situation-specific head -rocking when begging for food shown by DmW) was dramatically affected by the change in environment, completely disappearing following release onto the island, then resuming on return to the laboratory.

## SUMMARY

The transfer from the laboratory onto a natural island resulted in many changes in the social behaviour of the chimpanzees in the present study. The chimpanzees were able to split into separate subgroups for travel in the larger area. Partner preferences were evident, some based on previous familiarity at the laboratory, others having developed following release. The sizes of subgroups showed trends similar to data from wild populations. The trend for male-male bonding was similar to wild data, but female-female bonding remained stronger than bonding between wild females. Over 2 island study periods for Group 1, there was an increase in group cohesiveness and a decrease in solitary travel.

There was a marked decrease in aggressive behaviour following release. There could be different explanations for this. For example, it could be a result of an increase in both space and complexity of the environment, which made it easier to avoid aggressive attack. The method of provisioning on the island also helped to reduce aggression. At the laboratory, food was thrown into enclosures with attempts to throw food to specific individuals. Squabbles over food often ensued, however. On the island, however, food was given directly to each group member, which reduced fights over food. Feeding time, however, was still the time when most aggression occurred.

Trends in support by different age/sex classes during aggressive encounters were evident, with a tendency to support the same sex. Female-female support was stronger than that reported for wild females.

For Group 1, there was an increase in grooming frequency following release. This appeared to be related to the fact that grooming occurred most often following reunion of subgroups who had been travelling separately, a situation which can only occur in free- or semi-free-ranging populations.

There was an overall decrease in frequency of social play, but this was mainly due to a drop in adult social play frequency, which more closely resembles wild data.

Two types of behaviour seen for the first time following release in relation to sexual behaviour were interference of copulations and consort behaviour. Interference of copulations showed similarities to data from wild chimpanzees. Although there were only 2 examples of consort behaviour, it was interesting that this behaviour developed when an increase in ranging area made it possible.

There were also some changes in stereotyped behaviour. Stereotypic rocking stopped completely following release. Changes in an individual's behaviour could be dramatic, for example, *Trokon* who showed 4 types of stereotyped behaviour at the laboratory stopped these completely as soon as he was released. Other types of stereotypic or abnormal behaviour (which were generally more situation-specific), continued, however.

Overall, the members of the study group showed many changes in behaviour, some of which became more similar to the behaviour of free-ranging chimpanzees. Although the study group was limited in travel-range, and was still influenced by humans in some ways, in particular by provisioning, many changes in behaviour were encouraging, in particular that they occurred even after many years in captivity. Most of these changes could also subjectively be called "improvements", and certainly none were detrimental to the group. These are encouraging results both for rehabilitation projects, and for general improvements of captive environments for chimpanzees.

# CHAPTER 8

## DISCUSSION AND CONCLUSIONS

### Summary of Primate Release Projects

Comparison of the present study with other primate release projects is in many ways limited by the lack of data on the outcome of some primate release projects (Table 1.2). Most of the macaque release projects were translocations of wild-caught macaques either to another free-ranging area (e.g. KAWAI, 1960; BERTRAND, 1969; SOUTHWICK et al, 1984) or to an island (e.g. CARPENTER, 1942; MORRISON & MENZEL, 1977). Most projects involved provisioning after the transfer. Although no specific figures are given, all the macaque projects seemed to be fairly successful, which is perhaps not surprising considering they were all wild-born, and most of them had spent little (maximum of 1 year) or no time in captivity. They therefore already had the skills necessary for surviving in a natural environment.

The next group of projects in Table 1.2, the gibbon releases, were less successful. All 3 island release projects were discontinued, 2 after 50 % and 60 % mortality (BERKSON et al., 1971; BALDWIN &TELEKI, 1976). In the 1 gibbon release project which involved releasing gibbons into a free-ranging site (TINGPALAPONG et al., 1981), the success rate was not known, because the majority were not seen more than 1 month after release. There was no mention of pre-release training for this project, although 2 gibbons had been part of an earlier island release project. Some of the gibbons who had spent many years in captivity or who were captive-born could not be expected to adapt readily to release into a free-ranging site. The success rate of the project was therefore likely to be low.

The last group of projects in Table 1.2 had varying degrees of success. Despite the confusion from differing reports on the squirrel monkey (*Saimiri sciurens*) island release (TSALICKIS, 1972; BAILEY et al, 1974), overall the project does not seem to have been successful.

WILSON'S (1980) project releasing vervet monkeys (*Cercopithecus pygerythrus*) onto an island appears to have been more successful. WILSON had given these monkeys pre-release training in foraging and in predator avoidance. The baboon translocation project described by STRUM & SOUTHWICK (1986) can be considered successful. In this case the baboons had only to adapt to a new, but similar free-ranging site, using skills already developed. The baboons were closely monitored following the translocation and were initially provisioned. The baboons successfully adapted to the new environment and also natural patterns of transfers between the translocated and indigenous troops developed.

The final project of Table 1.2, the release of mainly captive-born golden lion tamarins, can be considered one of the least successful, but this may be only because of lack of follow-up data from some of the other projects. The captive-born tamarins were very limited in their ability to adapt to a new environment despite pre-release training, particularly the adults. In this respect, the monkeys seemed more "hard-wired" in their responses, in contrast to the flexibility of response and ability to adapt to new environments shown by great apes in the projects outlined in Tables 1.3 and 1.4 and discussed below.

Summary of great ape release projects

Although accurate figures are not available for the number of orang-utans successfully rehabilitated in the projects listed in Table 1.3, in general the orang-utan projects seem to be more successful than chimpanzee release projects (Table 1.4), if the final goal is to release apes into free-ranging sites. This has been done with orang-utans, but not with chimpanzees. BREWER (1982) attempted to release chimpanzees into a free-ranging site, but after continual attacks by wild chimpanzees in the area who were apparently seeking out the rehabilitated chimpanzees, BREWER decided to move them to an island in the River Gambia , where they still remain.

There have also been more reports of aggression towards humans in chimpanzee rehabilitation projects than in orang-utan projects, particularly in relation to the numbers of apes in these projects. From the literature on orang-utan rehabilitation projects, there are only a few reports of orang-utans becoming aggressive towards humans. De SILVA (1971) reported that an adult male orang-utan once attacked a man. RIJKSEN & RIJKSEN-GRAATSMA (1975) mentioned an adolescent female who was becoming unmanageable and showing signs of aggression towards humans. GALDIKAS (1980) also mentioned an adolescent male who was becoming increasingly aggressive, particularly towards human males. Both of these adolescents were transferred to areas of forest far from the rehabilitation centres.

Although it is difficult to compare the difference quantitatively, aggression by rehabilitated chimpanzees towards humans seems to be more common and more severe than that reported for rehabilitated orang-utans. It was difficult for humans to walk on Rubondo island in Tanzania, following the release of chimpanzees there (GRZIMEK, 1970), which was not surprising because these chimpanzees already had a reputation for aggression towards humans before their release. An adult male released there continually sought out and attacked a game warden living on the island, until he was shot (by a second warden) during a vicious attack,during which the warden lost 1 finger and a piece of flesh from 1 leg (GRZIMEK, 1970). A second adult male chimpanzee on Rubondo island may also have been shot for the same reason (BORNER, 1985). Second and third generation chimpanzees born on Rubondo who have had little or no contact with humans tend to avoid humans, behaving like unhabituated wild chimpanzees (BORNER, 1985).

BREWER (1982 : 266) reported an adolescent male chimpanzee attacking a new researcher joining the rehabilitation project and biting off a piece of her ear. CARTER (1988) also described a young adult male (whom she had known since infancy) charging at her and dragging her though a bush, after which she did not walk on the release island. In the present study , some members of the study group (see Chapter 4), and previously released groups (PRINCE et al, 1985, ZEONYUWAY, pers. comm.) were aggressive towards humans, and seemed to become increasingly so after release. Most aggression was shown by members of the first group of chimpanzees released by Vilab between 1978 and 1980. It was no longer possible for humans to safely walk on this island in 1980, although some of these chimpanzees may already have been particularly aggressive towards people when released (BROTMAN, pers. comm.). Another difference with this group was that they were released onto an island where people both in canoes and in power boats frequently pass. People passing have been seen to stop and call the chimpanzees. The chimpanzees then come, perhaps in response to hearing a boat motor and expecting to be fed. On arriving and not being fed, however, the chimpanzees become frustrated. This may be one reason why these chimpanzees have become particularly aggressive towards people.

Aggression towards humans by released apes is obviously a problem not only for humans attempting to carry out follow-up studies, but also for any humans released apes should come into contact with. A release site would therefore have to be sited far from any inhabited areas, or preferably separated by natural barriers such as rivers, to reduce the possibility of chimpanzees travelling from the release site to inhabited areas.

For released chimpanzees, aggression from wild chimpanzees could also be a problem, based on BREWER'S (1982) experience (see above), and also based on the fact that aggression occurs between wild communities of chimpanzees (GOODALL et al.,1979), with some examples of members of one community killing members of another (NISHIDA et al., 1985). Unless rehabilitated chimpanzees were released in large (30-50 individuals) cohesive groups, particularly with adult male group members, their chances of becoming established in a free-ranging area with neighbouring resident wild populations would not be favourable. They would also be disadvantaged in being unfamiliar with the area when first released. This is another reason why chimpanzees in the projects listed in Table 1.4 have been released onto islands rather than free-ranging sites.

Orang-utans, however, show differences in aggression both towards conspecifics and humans, and have been successfully released into free-ranging sites where wild orang-utans occur. This difference can be explained by differences in social structure between orang-utans and chimpanzees. Orang-utans are widely spaced and mostly solitary, and although solitary adult male orang-utans exclude other adult or adolescent males from their territory, there are no reports of joint attacks by wild orang-utans as has been described between different populations of wild chimpanzees (NISHIDA et al., 1985) and by wild chimpanzees towards released chimpanzees (BREWER, 1982). Chimpanzees could be released onto islands large enough (perhaps as large as the minimum range of wild populations, e.g. see BALDWIN et al., 1981) for them to become totally self-sufficient (which would also require detailed surveys on vegetation types and available food), and therefore not require any human contact, as with the Rubondo release group. The next generation of chimpanzees born on the island would then probably avoid humans, as has occurred on Rubondo island (BORNER, 1985). This could therefore eliminate the problem of aggression towards humans, but if these chimpanzees were then released into free-ranging sites where wild chimpanzees occurred, then there would still be the possibility of attack by wild chimpanzees. If sites were chosen for paucity or absence of wild chimpanzees, this problem could also be eliminated, but at the same time this would rule out the possibility of female transfer to other populations as occurs in wild populations (e.g. see PUSEY 1979, 1980). The chimpanzees, therefore, although no longer on an island would be a 'genetic island', in the sense that there would be no possibility of genetic transfer between neighbouring populations. This might eventually lead to problems of inbreeding within the released population.

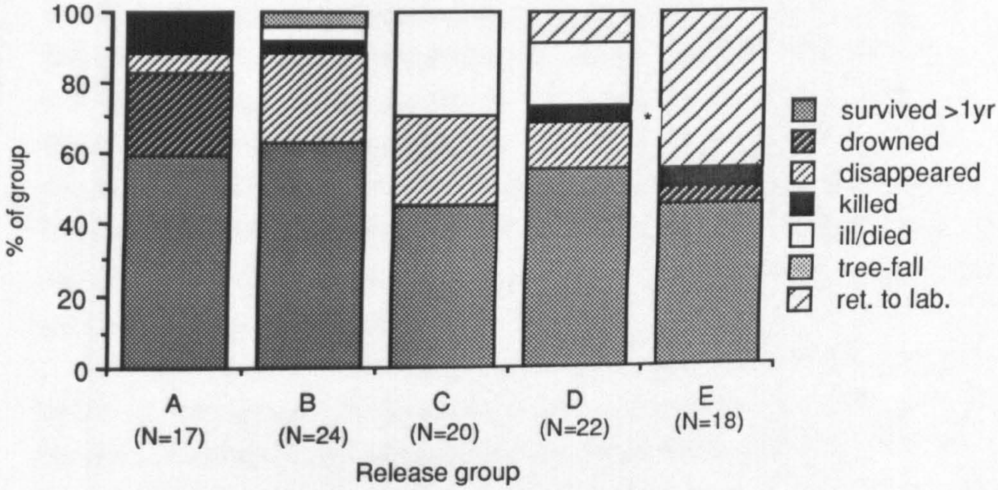
<u>Comparison of study-group with previously released Vilab groups</u>

Data on the outcome of 5 groups of chimpanzees released from Vilab onto islands between 1978 and 1987 are illustrated in Figure 8.1. The proportion of chimpanzees who survived for more than 1 year on an island varies from 45 % (Groups C & E) to 63 % (Group B), but the fate of those who did not survive varies between the groups. Group A was released onto the smallest island (5.5 ha), where there was less possibility of chimpanzees becoming lost or avoiding people, therefore there were fewer unexplained disappearances in this group than in subsequently released groups. In this group, however, a larger proportion of subjects were killed and 50 % of the subjects who drowned may have been forced off of the island during aggressive encounters. The reason for the larger proportion of deaths following aggression in this group, however, was much related to the fact that new subjects were added to the island up to 20 months after the first sub-group was released. From the end of 1979 to the middle of 1980, of 5 new additions to Group A, 4 males died and 1 female survived. Two of the males were killed and 2 were found drowned. Thereafter, no new additions were made to group A.

Group B was released onto Island A in 1983. At this time there was no canal separating Islands A and B from Island C, thus the total area available for the chimpanzees was over 100 ha (including mangrove areas). Twenty-five percent of this group disappeared following release and were not found. Four chimpanzees were added to this group 1 month after the first 20 were released. Of these 4, an adolescent female was killed by chimpanzees previously released, and 3 juveniles (2 females and 1 male) were successfully integrated into the group.

Group C had the largest proportion (30 %) of illnesses resulting in death following release. Most group members suffered from severe diarrhoea following release, and treatment of illnesses in this group was more difficult because they were released onto an island in Ivory Coast which was not near any medical facilities, whereas all other groups were released on islands within daily travelling distance from Vilab, and chimpanzees could be returned there for medical treatment. Also, 25 % of this group disappeared , which may have been a result of sick chimpanzees becoming lost and dying on the large (169 ha) island and not being found. For example, one individual who disappeared had diarrhoea when last seen (PRINCE et al., 1985).

**FIGURE 8.1** Fate of 5 Vilab groups of chimpanzees released onto islands.




A = 1st Vilab release group, released in Oct. 1978-July 1980 onto island D.
B = 2nd Vilab release group, released in May 1983 onto Island A (then transferred to Island C in May 1985).
C = 3rd Vialb release group, released in August 1983 (onto Island in Ivory Coast).
D = 4th Vilab release group = GROUP 1 of present study.
E = 5th Vilab release group = GROUP 2 of present study.

**Legends** :

survived >1yr = survived on island for more than 1 year
drowned = drowned offshore of island
disapp. = disappeared following release and body not found
killed = killed by other chimpanzees (* = from a different island group)
ill/died = illness which lead to death (on island or following return to laboratory)
tree-fall = death presumed to be a result of falling from a tree
ret. to lab. = returned to laboratory and survived there

Data on groups A-C are from PRINCE et al (1985)

Groups D & E of Figure 8.1 are Groups 1 and 2 of the present study. Although the number of chimpanzees who survived on the island in these groups did not increase in comparison to previously released groups, there were fewer (Group 1) or no (Group 2) disappearances, which was because there was an increase in proportion of the group fitted with radio-transmitter collars (see below). Eighteen percent of Group 1 became ill and died, whereas there were no deaths from illness in Group 2. There could be various explanations for this difference between Groups 1 and 2. For example, members of Group 2 had members of Group 1 to observe and learn from following release, and through this were probably less likely to make mistakes such as eating unsuitable foods. Also, during the study period both the author and laboratory staff learned to spot the early signs of illnesses (usually a decrease in appetite), and lethergy, and thus returned sick chimpanzees to the laboratory for treatment sooner, which gave an increased chance of recovery.

The large proportion (44 %) of Group 2 (Group E in Figure 8.1) returned to the laboratory was a result of aggressive attacks on members of Group 2 (mostly by members of Group 1). All of these transfers to the laboratory occurred more than 1 month after release (and therefore when the author was no longer present). One adolescent male was found drowned and 1 juvenile male was found dead, with many wounds. All of the chimpanzees in Group 2 were wearing radio-transmitter collars and were therefore found even if they were avoiding the other chimpanzees after an aggressive encounter, and returned to the laboratory if necessary.

<u>Differences in release techniques for study group</u>

More details on the differences in release technique between the study groups and previously released groups are discussed in the following sections.

1) <u>Separate sub-groups for release</u> : Groups 1 and 2 were split into separate sub-groups for release (see Tables 4.1 and 4.2). This allowed closer monitoring of newly released subjects and reduced the possibility of subsequently released individuals becoming lost. Once members of the first sub-group knew the island, individuals who were released subsequently often travelled with the ones who already knew their way around. The first sub-group contained the younger and lower-ranking individuals. The younger group members were allowed to become used to the island before the release

of higher-ranking group members, which perhaps helped to reduce stress for the lower-ranking group members during their initial period of adaptation to the island.

Releasing groups in smaller sub-groups also made it easier to observe the progress of each individual and to find individuals who had become lost. Also, as well as relying on others' knowledge of the geography of the island, subsequently released sub-groups could learn from other experience gained by members of the first sub-groups released (discussed further below).

2) Cage at shore of Island A : The chimpanzees were transported anaesthetised to the island then locked in the cage at the feeding site to recover. They were also kept in the cage overnight so that they could be let out early in the morning and observed throughout the day. This allowed time to find individuals who had wandered off alone and become lost. The cage also made it easier to add more individuals to the island as chimpanzees will often attack others recovering from tranquilization even when they know them. The cage allowed for safe recovery if there were already apes there. It also made it easier for individuals who had not lived together at the laboratory to become acquainted. In Group 1, the 3 oldest males (*Daniel, Sokomodo,* and *Brutus* were the last individuals to be released) had not been introduced to some of the younger group members before release, in order to avoid aggression in the relatively confined spaces of captivity. These males were kept in the cage for a week. During this period, the younger males of the group especially, came to the cage and acted submissively towards them. By the time the 3 were released a dominance hierarchy had already been established and there was no fighting.

Finally, anxious individuals used the cage as a sleeping site when first released. Two individuals (*Grace* and *DmW*) slept inside the cage, and two (*Blamah* and *Meryn*) slept on top of it. Before long, the 3 who remained on the island slept in trees like the others, but the familiarity of a cage may have helped them in their initial adjustment from captivity.

3) Radio-tracking : Before release 6 members of Group 1 and all members of Group 2 were fitted with radio-transmitter collars. This allowed them to be be tracked if they did not come to the feeding site on feeding days (which was every day when first released). The collars were especially useful in the beginning when the chimpanzees were finding their way around the island and learning to come to the feeding site when they heard a boat arrive. Animals were found by radio-tracking many times in the early weeks. Initially only 6 radio-collars were available (for Group 1), but optimal use was made of them by transferring them from members of the first sub-group released to some members of the next subgroup to be released, when possible. Collars were only

removed from individuals who were coming to the feeding site daily. Although only some group members were wearing collars, when they split into small subgroups for travelling usually at least one member of each party was wearing a collar. *Carolla* of Group 1 probably would not have survived had she not been wearing a collar. When first released she always travelled alone and had to be tracked every day before she finally learned to come to the feeding site. One day she sat in a tree calling continually until the author found her; she then followed the author to the feeding site. Four years later she is still living on an island (but now without a collar), travels with the others, comes to the feeding site on feeding days, and is successfully rearing an infant born on the island.

All members of Group 2 were wearing radio-collars when released, and there were therefore no unexplained disappearances in this group.

4) Closer supervision of release : The author also monitored released chimpanzees more closely than had been done previously. Hence, the island was visited every day after release, and whole days were spent there. The presence of familiar people (the author and laboratory staff) probably made a difference for the younger or more insecure group members. They followed humans until they knew their way around and felt confident about travelling on their own. Daily presence on the island also meant that illnesses were spotted and treated more quickly.

## COMPARISON OF 'FAILURES' AND 'SUCCESSES' IN STUDY GROUP

When the 'failures' and 'successes' of Group 1 (Table 8.1; Group 2 is not included because the author was only present for 2 months following release), in terms of the chimpanzees who did not survive or who were returned to captivity and those that remained on the island, are compared (with reference to such characteristics as sex, age at capture, age at release, and the number of years as a pet), there are no statistically significant differences between the two groups (Table 8.2). There is a trend, however, towards a sex difference in success rate. Of the original group of 22 a higher proportion of females successfully adapted than males. Note that *Hermaphrodite*, the adolescent male who was killed by another group after crossing the canal, is excluded from these calculations and 2 females who survived (*Popeye* and *Grace*) are excluded because of lack of data. If *Hermaphrodite* is included in the 'failure' group, the sex difference is significant (Fisher's exact probability, $p = 0.048$, 1-tailed). There are some data which suggest that females may have been more adaptable than the males. Females initiated behavioural patterns such as nut-cracking and ant eating. Also, when Groups 1 and 2

**TABLE 8.1** Fate of members of Group 1 following release.

| | Name | Sex | Age at capture | Age on release | No. yrs as pet | Sub-gp. reld. in | Radio-collared |
|---|---|---|---|---|---|---|---|
| 1a. | Cruella | f | 3.0 | 7.0 | 0 | 1 | |
| | Pim | m | 2.0 | 5.0 | 0 | 1 | |
| | Reagan | m | 3.0 | 7.5 | 0 | 1 | |
| 1b. | DmW | f | 1.5 | 8.5 | 4.0 | 2 | (x)+ |
| | Franco | m | 1.0 | 9.5 | 4.0 | 1 | + |
| 1c. | Daniel | m | 0.5 | 10.5 | 5.0 | 4 | |
| | Knut | m | 2.0 | 6.5 | >1.0 | 1 | + |
| | Maki | f | 0.5 | 9.5 | 0 | 3 | |
| | Trokon | m | 0.5 | 8.5 | 3.0 | 1 | + |
| 1d. | Hermaphrodite | m | 0.75 | 5.5 | 0.25 | 1 | + |
| 2. | Blamah | f | 1.5 | 7.5 | 0.5 | 1 | |
| | Brutus | m | 1.0 | 8.5 | 3.0 | 4 | |
| | Carolla | f | 2.5 | 9.5 | 1.0 | 2 | (x)+ |
| | Goldilocks | f | 2.5 | 7.0 | 0.5 | 2 | |
| | Grace | f | ? | >20.0 | 0 | 3 | + |
| | Helen | f | 1.0 | 5.5 | 0.5 | 1 | |
| | Houdina | f | 3.0 | 9.5 | 4.0 | 2 | + |
| | Maria | f | 1.5 | 6.5 | 0.5 | 1 | + |
| | Meryn | m | 0.5 | 5.0 | 0 | 1 | + |
| | Popeye | f | ? | 6.5 | <1.0 | 1 | |
| | Samantha | f | 1.0 | 9.5 | 0 | 3 | + |
| | Sokomodo | m | 2.0 | 8.5 | >1.0 | 4 | |

**Group classification :**

1a = disappeared on first day of release
1b = returned to laboratory (and survived there)
1c = became ill and died
1d = crossed canal and was killed by chimpanzees on adjacent island
2 = survived on island for more than 1 year

(x)+ = not wearing a radio-collar when first released, but had one fitted at a later date.

**TABLE 8.2** Comparison of release Group 1 in terms of survival.

| | Sex | Mean age (y) at capture | Mean age(y) on release | Mean no. yrs as pet |
|---|---|---|---|---|
| **Non-survivors** | 6m,3f | 1.6 | 8.1 | 1.9 |
| **Survived >1yr** | 3m,9f | 1.7 | 7.7 | 1.1 |
| **Statistics** | F. prob., p=0.07 1-tailed | M-W, p=0.74 2-tailed | M-W, p=0.68 2-tailed | M-W, p=0.77 2-tailed |

F.prob. = Fishers exact probability test
M-W = Mann-Whitney U-test

Note : *Hermaphrodite* is not included in these calculations because he was killed by chimpanzees in another island group, and *Popeye* and *Grace* are not included because some data are not available for these 2 subjects.

were combined, and the nut-cracking capabilities of the 35 subjects (on whom nut-cracking data were available) were compared , there was a trend for females to be more successful than males in learning to crack nuts (Figure 6.10).

Success and failure of rehabilitation may also be compared with when individuals were released. Seven out of 10 "failures" were in the first sub-group released (Table 8.1). As previously mentioned, this can in part be explained by the fact that additional group members travelled together with chimpanzees who already know their way around the island and were therefore less likely to become lost. Of the 3 individuals who disappeared and were never found, all were members of the first sub-group released. One clear way to eliminate this kind of loss would be to release only radio-collared individuals in the first subgroup when starting a new release. Individuals who are added at a later date, can make use of the others' knowledge of the geography of the island, and can also observe which natural foods the others are eating, and how to obtain these foods. In other words they have models on which to base their behaviour.

In the end, however, likelihood of success or failure is probably related to a variety of factors for each individual. Perhaps with more systematic data from rehabilitation projects, the factors affecting the likelihood of success for each individual released may be clarified.

## Goals of rehabilitation projects

How we rate the success of a rehabilitation project depends on its original goals. For example if release of captive primates into free-ranging sites, self-sufficiency, and interaction with wild conspecifics were expected, this goal has not been achieved yet in any chimpanzee rehabilitation project, but has been to some extent in orang-utan rehabilitation projects. If the aim is to improve the environment for captive primates by release into semi-free ranging sites (such as islands) where at least partial provisioning is necessary, this has been successful for some individuals in each of the chimpanzee island release projects listed in Table 1.4. In the present study, many changes in behaviour following release were beneficial, such as a decrease in aggression and in stereotyped behaviour, and the chimpanzees showed many forms of natural behaviour not exhibited at the laboratory.

If the individual well-being of primates who have survived and adapted to their change in environment is balanced against mortality of others who did not survive, decisions on the degree of success of a project may still be problematical. The present study has shown, however, that improvements can be made in release technique which can help to reduce mortality. Prospects may therefore improve for future releases of chimpanzees onto islands. Whether island-living chimpanzees in this and other projects will ever be released into free-ranging sites still remains open to question however.

## Recommendations for future releases and future research

Techniques which can be usefully applied in primate release projects will vary, depending on factors such as release site, the species to be released, and backgrounds of the individual primates. Some general recommendations can be made, however, some based on techniques used in this study, and some further developments of techniques used in this study. These general recommendations are as follows :

Pre-release preparation

Release subjects should be introduced and kept together for as long as possible prior to release, for example, a minimum of 6 months, or preferably 1 year. The 3 subjects of the present study who disappeared immediately following release were all added to the release froup only 1 month before release. Other subjects who were added to the release group 1 month before release survived and travelled with the others, but the 3 subjects who disappeared may well have been less likely to travel on their own if they had been more integrated into the group before release. Subjects should be kept in appropriate groups in captivity, depending on the social structure of the species. Any subjects who have been kept in isolation should first be resocialised before addition to a release group.

Subjects should also be kept in as complex an environment as possible while in captivity. This is particularly important for arboreal species which require skills in dealing with many different vegetation types in a natural forest. KLEIMAN et al. (1988) report on the inability of released golden lion tamarins to use vegetation types of different width and flexibility, and their inability to plan routes through the forest. Mainly terrestrial species should also be given the opportunity to climb in captivity, as this skill may be important in order to climb to food sources or sleeping sites. Opportunities should also be given to sleep in appropriate locations in captivity, e.g. above ground, or in hides. Nesting materials should also be provided.

If possible release subjects should be given wild foods to eat prior to release, particularly species known to occur in the prospective release site. Amount of wild foods given could be increased immediately prior to release, so that change in diet will be gradual. Subjects should also be provisioned following release, then degree of provisioning gradually decreased if appropriate.

If any form of training can be given prior to release which may help subjects to adapt to their new environment, this should be attempted. For example, if special techniques are required for obtaining particular foods, these should be demonstrated to subjects prior to release. This may not be necessary for some wild-born subjects, and these subjects can then serve as role models for other group members. Subjects could also be discouraged from eating unsuitable foods, and given some training in predator avoidance.

Choice of release site

As discussed previously in this chapter, there are different considerations to take into account when choosing a release site. For example, the absence of indigenous conspecifics and areas inhabited by humans. The carrying cpacity of the area in terms of food supply at all times of year should also be determined before release.

A 'base' from which subjects can orient themselves seems to have been useful in some primate release projects. TINGPALAPONG et al. (1981) reported a release of 30 gibbons into a free-ranging site in Thailand. The gibbons were released in two different ways. Fifteen gibbons were first released into cages in the forest, and could return to these cages after release for provisioning. The other 15 were released directly into the forest with no base to return to. Ten of the 15 gibbons released first into cages were seen periodically returning to these cages for food during the first week after release, whereas most of the 15 gibbons released directly into the forest were not seen at all after release. A base to which released subjects can return therefore helps both in monitoring released subjects, and may also help released individuals in their adaptation to a new environment . Individuals who are not finding enough to eat have the option of returning to a base for provisioning, and having a familiar base to return to may also provide security for released subjects in their new environment. STRUM (STRUM & SOUTHWICK, 1986) also used cages to orient translocated troops of baboons to the unfamiliar release area.

Release and follow-up procedures

Radio-transmitters should be fitted to all release subjects if there is any likelihood of subjects becoming lost, or if the release area is large enough so that subjects could easily avoid people if they chose to. Even if subjects are expected to become totally self-sufficient, radio-transmitters will allow monitoring of subjects after release, and thus help in the determination of the success of the release. Some orang-utans released into free-ranging sites (e.g. BORNER, 1979) were reported to have been successfully rehabilitated when they left the rehabilitation centre, even when there were no data to confirm they were successfully living in the forest. Radio-transmitters therefore allow better determination of successful rehabilitation for each individual. Daily monitoring of subjects should be carried out immediately following release, and for as long as necessary. The early stages of release is a time when subjects may be vulnerable to illnesses, and daily monitoring will allow early diagnosis of illness. If subjects become ill, appropriate medical treatment should be given, either at the release area (e.g. by giving oral medication), or if necessary the subject could be caged at the release area for as long as necessary, or temporarily taken to a facility where medical treatment and closer observation is possible. The subject can then be re-released when recovered, or introduced to another release group.

Subjects should be released in small groups, which will allow monitoring of each subject. Social relationships should be taken into account when splitting a large group into smaller subgroups for release. For example, if subjects show partner preferences they should be released with their preferred partner. Lower-ranking group members should also be released first, to allow them to adjust to their new environment before release of higher-ranking group members.

Data should be collected on the progress of each individual following release, and if possible related to the individual's rearing history. Collection of such data, and comparison with pre-release data, may lead to improvements in pre-release training and in release procedures, which in turn can improve the success rate of future releases.

# APPENDIX A

## DEFINITIONS OF CATEGORIES OF BEHAVIOUR RECORDED

*Aggression* : data presented on aggression are encounters which involved contact of an agonistic nature between subjects. That is, one subject hit, jumped on, slapped, or bit another subject. The victim of the attack usually screamed, and showed an open-mouth fear grin.

*Grooming* : Subject looks through own (*self-grooming*) or other subject's (*social grooming*), hair, using fingers and/or lips.

*Sexual behaviour* : copulation between male and female subject.

*Social play* : One subject chases (*play-chase*) or wrestles (*play-wrestle*) with another subject. Play usually clearly identified when subjects show 'play-face' (Van HOOFF, 1967 b).

*Stereotyped behaviour* : see Appendix C.

# APPENDIX B.

TABLE 1 (a)
Proximity data, subject group 1a. Scores are the percentage of samples in which the individuals were recorded in proximity.

| | D | So | H | Mk | Mf | P | S |
|---|---|---|---|---|---|---|---|
| Daniel (D) | | 11.2 | 5.4 | 4.5 | 12.9 | 6.2 | 7.6 |
| Sokomodo (So) | 11.2 | | 12.9 | 13.8 | 17.8 | 14.3 | 11.2 |
| * Hardtimes (H) | 5.4 | 12.9 | | 15.2 | 14.3 | 32.6 | 31.3 |
| Maki (Mk) | 4.5 | 13.8 | 15.2 | | 23.7 | 30.3 | 28.1 |
| * Ms. Fields (Mf) | 12.9 | 17.8 | 14.3 | 23.7 | | 25.4 | 23.7 |
| * Putukin (P) | 6.2 | 14.3 | 32.6 | 30.3 | 25.4 | | 29.0 |
| Samantha | 7.6 | 11.2 | 31.3 | 28.1 | 23.7 | 29.0 | |

TABLE 1 (b)
Contact data, subject group 1a. Scores are the percentage of samples in which the individuals were recorded in contact.

| | D | So | H | Mk | Mf | P | S |
|---|---|---|---|---|---|---|---|
| Daniel (D) | | 1.3 | 2.7 | 0.4 | 1.3 | 0 | 0.4 |
| Sokomodo (So) | 1.3 | | 1.3 | 0 | 1.3 | 0.8 | 2.7 |
| * Hardtimes (H) | 2.7 | 1.3 | | 3.6 | 0 | 0.4 | 10.7 |
| Maki (Mk) | 0.4 | 0 | 3.6 | | 0.8 | 0.4 | 0.8 |
| * Ms. Fields (Mf) | 1.3 | 1.3 | 0 | 0.8 | | 1.3 | 1.3 |
| * Putukin (P) | 0 | 0.8 | 0.4 | 0.4 | 1.3 | | 17.4 |
| Samantha | 0.4 | 2.7 | 10.7 | 0.8 | 1.3 | 17.4 | |

= not released

TABLE 2 (a)
Proximity data, subject group 1b. Scores are the percentage of samples in which the individuals were recorded in proximity.

| | Br | Hp | Tr | Dw | Hl | M |
|---|---|---|---|---|---|---|
| Brutus (Br) | | 26.8 | 1.2 | 24.1 | 17.9 | 8.9 |
| Hermaphrodite (Hp) | 26.8 | | 4.5 | 27.7 | 33.9 | 29.0 |
| Trokon (Tr) | 1.2 | 4.5 | | 9.8 | 8.0 | 3.6 |
| DmW (Dw) | 24.1 | 27.7 | 9.8 | | 35.3 | 20.5 |
| Helen (Hl) | 17.9 | 33.9 | 8.0 | 35.3 | | 35.3 |
| Maria (M) | 8.9 | 29.0 | 3.6 | 20.5 | 35.3 | |

TABLE 2 (b)
Contact data, subject group 1b. Scores are the percentage of samples in which the individuals were recorded in contact.

| | Br | Hp | Tr | Dw | Hl | M |
|---|---|---|---|---|---|---|
| Brutus (Br) | | 3.1 | 4.9 | 0.8 | 3.1 | 0 |
| Hermaphrodite (Hp) | 3.1 | | 1.3 | 5.8 | 2.7 | 0.4 |
| Trokon (Tr) | 4.9 | 1.3 | | 0.4 | 0.8 | 0 |
| DmW (Dw) | 0.8 | 5.8 | 0.4 | | 3.6 | 0 |
| Helen (Hl) | 3.1 | 2.7 | 0.8 | 3.6 | | 1.8 |
| Maria (M) | 0 | 0.4 | 0 | 0 | 1.8 | |

TABLE 3(a) Proximity data, subject group 1d. Scores are the percentage of samples in which the individuals were recorded in proximity.

| | G | C | Go | Ho |
|---|---|---|---|---|
| Ginger (G) | | 39.4 | 8.8 | 14.9 |
| Carolla (C) | 39.4 | | 16.2 | 34.6 |
| Goldilocks (Go) | 8.8 | 16.2 | | 16.7 |
| Houdina (Ho) | 14.9 | 34.6 | 16.7 | |

TABLE 3(b) Contact data, subject group 1d. Scores are the percentage of samples in which the individuals were recorded in contact.

| | G | C | Go | Ho |
|---|---|---|---|---|
| Ginger (G) | | 0.8 | 0 | 2.6 |
| Carolla (C) | 0.8 | | 1.3 | 3.5 |
| Goldilocks (Go) | 0 | 1.3 | | 2.2 |
| Houdina (Ho) | 2.6 | 3.5 | 2.2 | |

TABLE 4 (a) Proximity data for subject group 1d (with some members of subject group 1b*). Scores are the percentage of samples in which the individuals were recorded in proximity.

| | F | Hp | K | Mn | P | R | Tr | Bl | Cr | Hl | M | Po |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Franco (F) | | 31.9 | 2.1 | 25.0 | 6.3 | 7.6 | 6.3 | 11.1 | 5.2 | 20.1 | 23.6 | 4.2 |
| * Hermaph- rodite (Hp) | 31.9 | | 2.8 | 20.8 | 5.2 | 9.0 | 1.4 | 7.6 | 10.4 | 28.5 | 40.3 | 2.1 |
| Knut (K) | 2.1 | 2.8 | | 5.6 | 9.4 | 6.9 | 7.6 | 15.3 | 7.3 | 9.7 | 8.3 | 10.4 |
| Meryn (Mn) | 25.0 | 20.8 | 5.6 | | 11.5 | 6.3 | 8.3 | 11.1 | 6.3 | 18.8 | 28.5 | 10.4 |
| Pim (P) | 6.3 | 5.2 | 9.4 | 11.5 | | 6.3 | 9.4 | 10.4 | 25.0 | 8.3 | 11.5 | 8.3 |
| Reagan (R) | 7.6 | 9.0 | 6.9 | 6.3 | 6.3 | | 5.6 | 11.1 | 7.3 | 11.8 | 9.0 | 15.6 |
| * Trokon (Tr) | 6.3 | 1.4 | 7.6 | 8.3 | 9.4 | 5.6 | | 4.2 | 6.3 | 6.3 | 4.9 | 7.3 |
| Blamah (Bl) | 11.1 | 7.6 | 15.3 | 11.1 | 10.4 | 11.1 | 4.2 | | 10.4 | 10.4 | 16.0 | 7.3 |
| Cruella (Cr) | 5.2 | 10.4 | 7.3 | 6.3 | 25.0 | 7.3 | 6.3 | 10.4 | | 9.4 | 14.6 | 14.6 |
| * Helen (Hl) | 20.1 | 28.5 | 9.7 | 18.8 | 8.3 | 11.8 | 6.3 | 10.4 | 9.4 | | 39.6 | 13.5 |
| * Maria (M) | 23.6 | 40.3 | 8.3 | 28.5 | 11.5 | 9.0 | 4.9 | 16.0 | 14.6 | 39.6 | | 10.4 |
| Popeye (Po) | 4.2 | 2.1 | 10.4 | 10.4 | 8.3 | 15.6 | 7.3 | 7.3 | 14.6 | 13.5 | 10.4 | |

TABLE 4 (b) Contact data for subject group 1d (with some members of subject group 1b*). Scores are the percentage of samples in which the individuals were recorded in contact.

| | F | Hp | K | Mn | P | R | Tr | Bl | Cr | Hl | M | Po |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Franco (F) | | 0 | 0 | 0 | 0 | 0 | 0.7 | 0 | 0 | 0 | 0 | 0 |
| * Hermaphrodite (Hp) | 0 | | 0 | 1.4 | 0 | 2.1 | 0 | 0 | 8.3 | 0.7 | 2.7 | 0 |
| Knut (K) | 0 | 0 | | 1.4 | 0 | 1.4 | 4.2 | 0.7 | 1.0 | 0.7 | 3.5 | 0 |
| Meryn (Mn) | 0 | 1.4 | 1.4 | | 9.4 | 2.1 | 2.8 | 0 | 0 | 4.2 | 0 | 2.1 |
| Pim (P) | 0 | 0 | 0 | 9.4 | | 1.0 | 3.1 | 0 | 3.1 | 0 | 0 | 0 |
| Reagan (R) | 0 | 2.1 | 1.4 | 2.1 | 1.0 | | 4.9 | 0 | 2.1 | 5.6 | 6.7 | 1.0 |
| * Trokon (Tr) | 0.7 | 0 | 4.2 | 2.8 | 3.1 | 4.9 | | 0.7 | 1.0 | 0 | 0 | 0 |
| Blamah (Bl) | 0 | 0 | 0.7 | 0 | 0 | 0 | 0.7 | | 1.0 | 0 | 0 | 1.0 |
| Cruella (Cr) | 0 | 8.3 | 1.0 | 0 | 3.1 | 2.1 | 1.0 | 1.0 | | 0 | 0 | 1.0 |
| * Helen (Hl) | 0 | 0.7 | 0.7 | 4.2 | 0 | 5.6 | 0 | 0 | 0 | | 0 | 6.3 |
| * Maria (M) | 0 | 2.7 | 3.5 | 0 | 0 | 0.7 | 0 | 0 | 0 | 0 | | 0 |
| Popeye (Po) | 0 | 0 | 0 | 2.1 | 0 | 1.0 | 0 | 1.0 | 1.0 | 6.3 | 0 | |

TABLE 5 (a) Proximity data, subject groups 2a and 2b.
Scores are a percentage of samples in which the individuals were recorded in proximity.

| | Subject group 2a | | | | | | | | | | Subject group 2b | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | Mn | T | A | Bt | Mb | Mf | N | Tp | Tw | Dr | Wf | Bh | Bs | Te |
| Bill (B) | | 7.7 | 6.1 | 2.2 | 5.8 | 4.8 | 4.8 | 3.2 | 3.5 | 7.0 | 0 | 5.0 | 1.7 | 0 | 6.7 |
| * Meryn (Mn) | 7.7 | | 4.4 | 6.5 | 8.5 | 8.9 | 13.2 | 5.0 | 8.2 | 14.1 | 4.5 | 2.3 | 3.4 | 3.4 | 9.1 |
| Tolkein (T) | 6.1 | 4.4 | | 7.6 | 8.8 | 4.2 | 13.5 | 30.9 | 5.0 | 3.1 | 6.8 | 0 | 1.1 | 0 | 10. |
| Anita (A) | 2.2 | 6.5 | 7.6 | | 4.4 | 9.3 | 8.5 | 13.8 | 14.4 | 12.9 | 1.1 | 1.1 | 6.8 | 1.1 | 1.1 |
| Bertha (Bt) | 5.8 | 8.5 | 8.8 | 4.4 | | 8.0 | 8.8 | 7.0 | 10.3 | 7.8 | 2.3 | 1.1 | 11.4 | 5.7 | 5.7 |
| Mabel (Mb) | 4.8 | 8.9 | 4.2 | 9.3 | 8.0 | | 7.0 | 5.4 | 11.2 | 5.4 | 3.3 | 1.6 | 5.0 | 5.0 | 0 |
| Moffit (Mf) | 4.8 | 13.2 | 13.5 | 8.5 | 8.8 | 7.0 | | 10.3 | 8.8 | 12.5 | 3.4 | 0 | 5.7 | 4.5 | 7.9 |
| Natasha (N) | 3.2 | 5.0 | 30.9 | 13.8 | 7.0 | 5.4 | 10.3 | | 4.1 | 7.0 | 10.2 | 1.1 | 3.4 | 0 | 3.4 |
| Tipsy (Tp) | 3.5 | 8.2 | 5.0 | 14.4 | 10.3 | 11.2 | 8.8 | 4.1 | | 6.6 | 3.4 | 0 | 9.1 | 5.7 | 7.9 |
| Twebo (Tw) | 7.0 | 14.1 | 3.1 | 12.9 | 7.8 | 5.4 | 12.5 | 7.0 | 6.6 | | 0 | 0 | 0 | 0 | 0 |
| Dr. Me (Dr) | 0 | 4.5 | 6.8 | 1.1 | 2.3 | 3.3 | 3.4 | 10.2 | 3.4 | 0 | | 5.6 | 4.5 | 1.1 | 2.2 |
| olfram (Wf) | 5.0 | 2.3 | 0 | 1.1 | 1.1 | 1.6 | 0 | 1.1 | 0 | 0 | 5.6 | | 1.1 | 10.2 | 0 |
| Bahnti (Bh) | 1.7 | 3.4 | 1.1 | 6.8 | 11.4 | 5.0 | 5.7 | 3.4 | 9.1 | 0 | 4.5 | 1.1 | | 4.5 | 9.1 |
| Big Sore (Bs) | 0 | 3.4 | 0 | 1.1 | 5.7 | 5.0 | 4.5 | 0 | 5.7 | 0 | 1.1 | 10.2 | 4.5 | | 3.4 |
| Telle (Te) | 6.7 | 9.1 | 10.2 | 1.1 | 5.7 | 0 | 7.9 | 3.4 | 7.9 | 0 | 2.2 | 0 | 9.1 | 3.4 | |

TABLE 5 (b) Contact data, subject groups 2a and 2b.
Scores are a percentage of samples in which the individuals were recorded in contact.

| | Subject group 2a | | | | | | | | | | Subject group 2b | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | Mn | T | A | Bt | Mb | Mf | N | Tp | Tw | Dr | Wf | Bh | Bs | Te |
| Bill (B) | | 6.7 | 0.3 | 0.6 | 5.1 | 1.6 | 0.6 | 0 | 0.6 | 2.2 | 4.5 | 0 | 1.1 | 0 | 0 |
| * Meryn (Mn) | 6.7 | | 1.8 | 1.5 | 3.5 | 0.3 | 4.7 | 0 | 1.5 | 2.3 | 4.5 | 3.4 | 8.0 | 1.1 | 1.1 |
| Tolkein (T) | 0.3 | 1.8 | | 0.6 | 1.8 | 1.0 | 3.2 | 6.2 | 1.5 | 0 | 1.1 | 0 | 2.3 | 0 | 3.4 |
| Anita (A) | 0.6 | 1.5 | 0.6 | | 0.9 | 2.6 | 0.3 | 1.8 | 5.6 | 0 | 2.3 | 2.3 | 2.3 | 0 | 0 |
| Bertha (Bt) | 5.1 | 3.5 | 1.8 | 0.9 | | 0.6 | 0.9 | 0.6 | 3.5 | 2.0 | 4.5 | 0 | 1.1 | 1.1 | 2.3 |
| Mabel (Mb) | 1.6 | 0.3 | 1.0 | 2.6 | 0.6 | | 1.6 | 1.3 | 2.2 | 0.8 | 1.1 | 0 | 2.3 | 1.1 | 0 |
| Moffit (Mf) | 0.6 | 4.7 | 3.2 | 0.3 | 0.9 | 1.6 | | 0 | 1.5 | 4.7 | 4.5 | 2.3 | 1.1 | 2.3 | 1.1 |
| Natasha (N) | 0 | 0 | 6.2 | 1.8 | 0.6 | 1.3 | 0 | | 0.6 | 1.6 | 2.3 | 0 | 1.1 | 2.3 | 0 |
| Tipsy (Tp) | 0.6 | 1.5 | 1.5 | 5.6 | 3.5 | 2.2 | 1.5 | 0.6 | | 0 | 9.1 | 2.3 | 1.1 | 1.1 | 0 |
| Twebo (Tw) | 2.3 | 2.3 | 0 | 0 | 2.0 | 0.8 | 4.7 | 1.6 | 0 | | 0 | 0 | 0 | 0 | 0 |
| Dr. Me (Dr) | 4.5 | 4.5 | 1.1 | 2.3 | 4.5 | 1.1 | 4.5 | 2.3 | 9.1 | 0 | | 5.7 | 3.4 | 3.4 | 3.4 |
| Wolfram (Wf) | 0 | 3.4 | 0 | 2.3 | 0 | 0 | 2.3 | 0 | 2.3 | 0 | 5.7 | | 2.3 | 2.3 | 5.7 |
| Bahnti (Bh) | 1.1 | 8.0 | 2.3 | 2.3 | 1.1 | 2.3 | 1.1 | 1.1 | 1.1 | 0 | 3.4 | 2.3 | | 1.1 | 1.1 |
| Big Sore (Bs) | 0 | 1.1 | 0 | 0 | 1.1 | 1.1 | 2.3 | 2.3 | 1.1 | 0 | 3.4 | 2.3 | 1.1 | | 0 |
| Telle (Te) | 0 | 1.1 | 3.4 | 0 | 2.3 | 0 | 1.1 | 0 | 0 | 0 | 3.4 | 5.7 | 1.1 | 0 | |

# APPENDIX C

## ETHOGRAM OF STEREOTYPED OR ABNORMAL BEHAVIOUR

Bizarre stand: an unusual stance, typically performed with one leg supporting the weight of the body while the other is flexed at the knee.

Clap hands: common usage.

Coprophagy: ingestion of feces.

Eye poking: poking of one or more fingers into the eye.

Feces spreading: spreading of feces on a surface with the hands and/or mouth. Frequently accompanied by coprophagy.

Flapping genitals: repetitive patting of own genitals. Typically observed in association with sticking out tongue.

Hair pulling: pulling out of own or another animal's hair.

Hand movements: complex movements of the hand. Typically accompanied by a fixed gaze at the hand.

Head banging: repetitive striking of the head against a surface.

Head shaking: repetitive shaking of the head.

Head wiping: repetitive stroking of the head. Typically follows wetting of the head.

Lip flip: flipping of the lower lip out and over the chin.

Posture: Bizarre posturing of body.

Raspberry vocalization: produced by pursing lips and spitting air.

Regurgitation: deliberate, repetitive regurgitation typically accomplished by lowering the head to the ground. The vomitus is retained within the mouth and reingested.

Rocking: Repetitive seated, bipedal, or quadrupedal rocking.

Self-clasp: clasping of own body.

Self-mutilate: biting, scratching, or picking at own body sufficient to cause injury.

Self-slap: repetitive slapping of own body, typically directed to head or thighs.

Stick out tongue: common usage.

Suck object: nonnutritive sucking of an object.

Suck penis: sucking of own or another animal's penis.

Suck self: sucking of own body, typically skin of abdomen.

Suck tongue: sucking of own tongue.

Urine drinking: drinking of own or another animal's urine.

Wet head: stereotypic wetting of head with water, typically accomplished by butting water device with head. Frequently followed by head wiping.

From WALSH et al. (1982; 316-317), based on observations of 91 laboratory chimpanzees.

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