

CHAPTER 4

LITERATURE REVIEW ON CHIMPANZEES - THEIR PAST, PRESENT AND BLEAK FUTURE

FREE-RANGING CHIMPANZEES

"It is my firm belief that unless we work together to change attitudes at all levels - from world leaders to the consumers of illegal bush meat - there will be no viable population of great apes in the wild within 50 years" (Dr Jane Goodall as cited in APE ALLIANCE 1998).

Phylogeny and distribution

Chimpanzees are part of the family Hominidae which encompasses all African apes and man and belongs to the order Primates (Ruvolo *et al.* 1991, Kingdon 1997). In contrast to monkeys which belong to the family Cercopithecoidea, all apes (and man) are tail-less. All chimpanzees belong to the genus *Pan* (Ruvolo *et al.* 1991, Kingdon 1997).

The genus *Pan* is divided into two species which are endemic to equatorial Africa. The one species is the "common" chimpanzee, *Pan troglodytes*, and the other species is the "pygmy" chimpanzee, *Pan paniscus*, or bonobo (McGrew 1989, Teleki 1989, 1994, Kortlandt 1997-1998). The genus *Pan* is confined to the African continent and the ranges of the two described species do not overlap (Gagneux *et al.* 2001).

Until recently *Pan troglodytes* was divided into three subspecies, namely (Latinen 1989, McGrew 1989, Teleki 1989, 1994, Erwin 1992, Gagneux *et al.* 2001):

Pan troglodytes troglodytes, Blumenbach, 1799

(Central African or bald chimpanzee)

Pan troglodytes schweinfurthii, Giglioli, 1872

(East African or long-haired chimpanzee).

Pan troglodytes verus, Schwarz, 1934

(West African, Upper Guinea, or masked chimpanzee)

Teleki (1989, 1994) describes the geographical range of the three *Pan troglodytes* subspecies as mutually exclusive. *Pan troglodytes verus* is prominent in western Africa and its historical range extended from the Gambia River area to the west bank of the Niger River (Teleki 1989). *Pan troglodytes troglodytes* occupied the central African range from the east bank of the Niger River to the west bank of the Ubangi and Congo River (Teleki 1989). *Pan troglodytes schweinfurthii* occupied a range from the east bank of the Ubangi River and along the north bank of the Congo River to Lake Victoria and Lake Tanganyika (Teleki 1989). Bonobos only occur south of the Congo River (Gagneux 2001). Up until today, the range of both species has decreased substantially (McGrew 1989, Teleki 1989, 1994, Goodall 1994b). Teleki (1989) gives their range limits at 13° North and 7° South, with Senegal Oriental being the north western edge of the species' distribution and Shaba-Katanga in the DRC being the southernmost point of the chimpanzee's distribution (McGrew 1989).

Teleki (1989) lists 25 African countries in which chimpanzees were known to occur. He divides them according to the range of the three formerly known chimpanzee subspecies into (1) western African countries, namely, Benin, Gambia, Togo, Burkina Faso, Guinea-Bissau, Senegal, Ghana, Mali, Ivory Coast, Sierra Leone, Liberia and Guinea (*Pan troglodytes verus*), (2) central African countries, namely Nigeria, Angola (Cabinda), Central African Republic, Equatorial Guinea, Congo, Cameroon and Gabon (*Pan troglodytes troglodytes*) and (3) east African countries, namely Burundi, Rwanda, Sudan, Tanzania, Uganda and Zaïre (DRC) (*Pan troglodytes schweinfurthii*). Of these 25 countries two are known or believed to no longer have any viable chimpanzee population (Guinea-Bissau and Burundi) while in four countries (Benin, Gambia, Togo and Burkina Faso) chimpanzees have already been extinct for a while (Teleki 1989).

Gagneux *et al.* (2001) used mitochondrial DNA sequences and hyper variable nuclear micro satellite markers to investigate blood and faecal samples of chimpanzees in western, central and eastern Africa. Their results indicated that there is at least one newly-discovered, reproductively isolated chimpanzee population that is genetically distinct enough to form a new subspecies, *Pan troglodytes vellerosus*. Figure 4.1 shows the distribution of the four *Pan troglodytes* subspecies currently described: The range of *Pan troglodytes vellerosus* extends from the eastern bank of the Niger River to the western bank of the Sanga River, thus coinciding with the northwestern part of the range of *Pan troglodytes troglodytes* (Teleki 1989, Gagneux *et al.* 2001). These findings indicate that some geographical barriers, in this case the Sanga River, are of greater importance as a barrier for chimpanzee gene flow than was previously thought (Gonder *et al.* 1997, Gagneux *et al.* 2001).

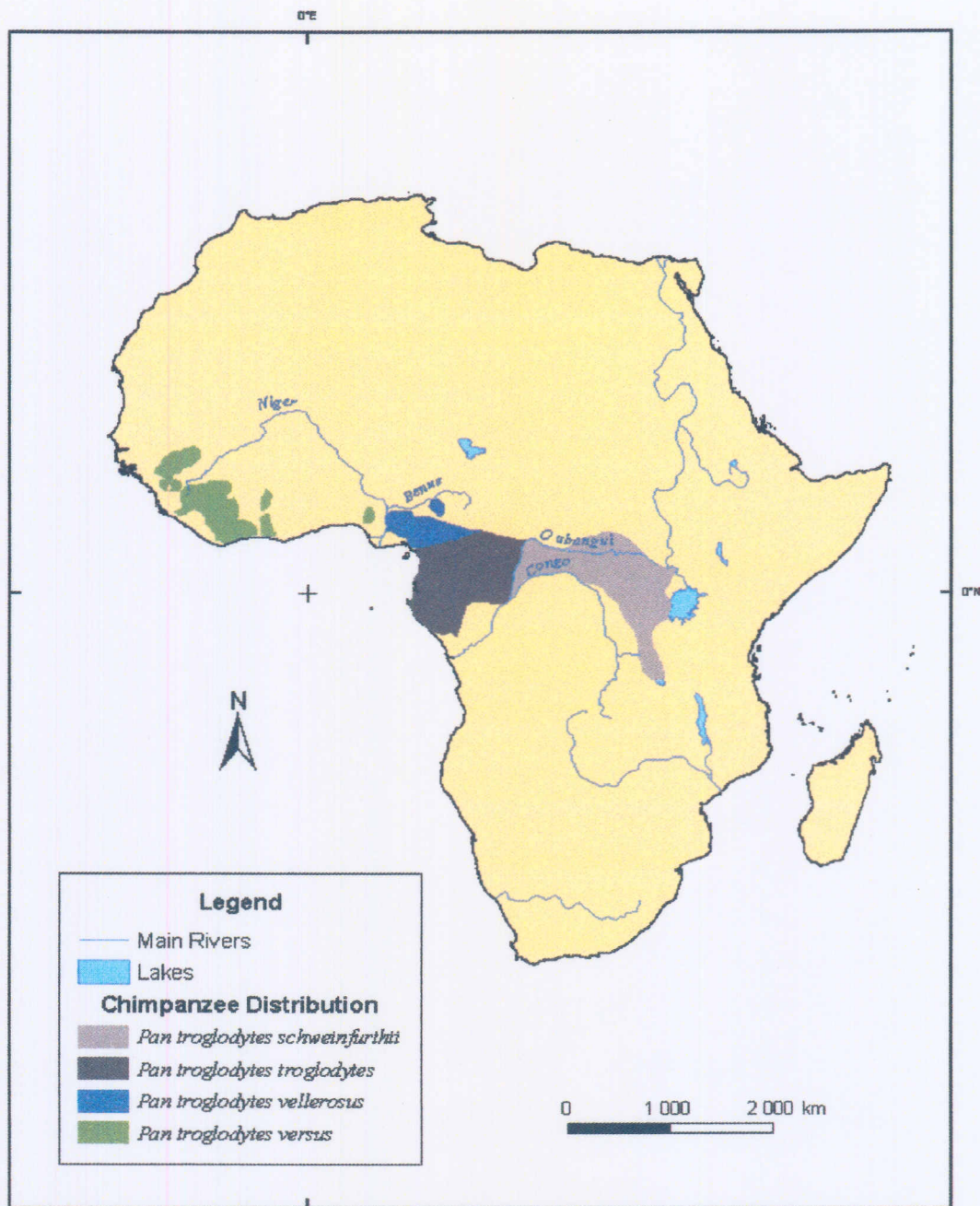


Figure 4.1: Distribution ranges of chimpanzee subspecies (Gagneux *et al.* 2001) – redrawn with kind permission from Pascal Gagneux.

At the same time, the results of the authors raised questions about the phylogenetic division of the eastern and western chimpanzee subspecies. Neither of the two subspecies forms monophyletic clusters with respect to each other. Some of the *Pan troglodytes troglodytes* sequences fall within the east African *Pan troglodytes schweinfurthii* sequences. This finding questions the Ubangi River as being a complete barrier between the ranges of the two subspecies, as was previously assumed (Teleki 1989, Gagneux *et al.* 2001). The authors state that extensive sampling of populations on either side of the river would be necessary to determine conclusively whether they are representatives of one or two subspecies (Gagneux *et al.* 2001). Gagneux *et al.* (2001) conclude that their findings indicate a more extensive gene flow between local chimpanzee populations than was previously thought and following patterns that are sometimes inconsistent with those documented through direct behavioural observations.

Mitochondrial DNA sequences allow conclusions about fairly recent events (tens to hundreds of thousands of years ago) in a species' evolution. On this time scale the authors determined an extensive within-subspecies gene flow for *Pan troglodytes schweinfurthii* and they consider this subspecies as having been panmictic at that point in time (Gagneux *et al.* 2001).

Current status and problems

"And what of the chimpanzees? ... But the question is purely academic. It could not be answered for countless thousands of years, and even *now* it is clear that the days of the great African forests are numbered. If the chimpanzees themselves survive in freedom, it will be in a few isolated patches of forest grudgingly conceded, where opportunities for genetic exchange between different social groups will be limited or impossible. And unless we act soon, our closest relatives may soon exist only in captivity, condemned, as a species, to human bondage" (Goodall 1998).

IUCN status and population size

The IUCN (2000a) lists chimpanzees, i.e. the genus *Pan*, as **endangered**, giving the exact status as: EN A 2cd. This categorisation is explained as follows (IUCN 2000b):

En	=	Endangered
A	=	with population reduction in form of:
2	=	at least 50%, projected or suspected to be met within the next 10 years or three generations, whichever is the longer, based on

- c = a decline in area of occupancy, extent of occurrence and/or quality of habitat, and
- d = actual or potential levels of exploitation.

Walter (pers. comm.⁴) gives the overall number of chimpanzees as 185 000 to 208 000, with about 2 500 of those animals officially registered as being held in captivity. The break down into subspecies / species is represented as follows (Walter pers.comm.):

<i>Pan troglodytes schweinfurthii</i> (East African Chimpanzee):	96 000
<i>Pan troglodytes troglodytes</i> (Central African Chimpanzee):	62 000
<i>Pan troglodytes verus</i> (West African Chimpanzee):	12 000 to 20 000
<i>Pan troglodytes vellerosus</i> (Nigeria Chimpanzee):	5 000
<i>Pan paniscus</i> (Bonobo):	10 000 to 25 000.

About 80 000 of those chimpanzees live in the Congo basin alone (Walter pers. comm.³) While *Pan troglodytes schweinfurthii* is the most abundant species in the wild, *Pan troglodytes verus* is the most abundant species in laboratories all over the world, but the second least abundant in the wild (Teleki 1989, Erwin 1992).

Chimpanzee study sites

A number of field studies have been undertaken on chimpanzee populations in Africa (Suzuki 1971, Baldwin & Teleki 1973, McGrew 1989, Teleki 1989, Goodall 1989, 1994a, Tutin & Fernandez 1991). Research into wild chimpanzees started as early as 1890 by R.L. Garner who built a cage in the west African jungle in which *he* could stay in safety while observing any chimpanzee passing by (Reynolds 1967, Goodall 1994b). Forty years later Henry Nissen continued studies in the wild in Guinea (Goodall 1994b).

Only at the beginning of the sixties did field research into wild chimpanzee populations start in earnest in eastern Zaire, Gombe, and Mahale Mountains on the eastern shore of Lake Tanganyika in Tanzania (Goodall 1994b). Soon afterwards research on chimpanzees in Uganda was started (Reynolds & Reynolds 1965a, Reynolds 1967, Suzuki 1969, 1971, Baldwin & Teleki 1973, Goodall 1994b). Research on chimpanzees subsequently spread to west and central Africa (Baldwin & Teleki 1973, Goodall 1994b). McGrew (1989) divides the field research on wild chimpanzees in West Africa into long-term and short-term studies, mentioning the study of the

⁴ Walter, M.2001. Jane Goodall Institute, Munich, Germany.

Taï Forest chimpanzees, Ivory Coast, as the most important long-term study of the 1980s. Another long-term study site of great importance for chimpanzee (and gorilla) research is in the Lopé Reserve in Gabon (McGrew 1989, Tutin & Fernandez 1991, Goodall 1994b).

At some field study sites protected areas have been opened for tourism, partly as an additional income-generating activity for the surrounding local communities and the governments of the respective home range countries, and partly to create public awareness and to raise additional income for the project through funding coming from foreign visitors (Goodall 1989, Grieser Johns 1996).

Just as chimpanzees have had to become habituated to primatologists wanting to study them (Tutin & Fernandez 1991) they also had to become habituated to the regular influx of tourist groups into their home range (Grieser Johns 1996). Male and female chimpanzees react differently to this disturbance. Male chimpanzees mainly show aggression to the unusual human intruder, while female chimpanzees mainly react with protective behaviour towards infants and juvenile chimpanzees, most likely their own offspring, or with flight reactions (Tutin & Fernandez 1991, Grieser Johns 1996). Eventually, when habituation has been completed, the chimpanzees hardly take any notice any longer of the presence of the visiting tourist or scientist (Grieser Johns 1996, Goodall 1998).

This close encounter between non-human and human primates constitutes a significant health risk, mainly for the chimpanzee. Strict rules have to be complied with, e.g. regarding a minimum distance which has to be kept between the observer and the habituated chimpanzee(s), or regarding waste disposal of any kind by the tourists while in chimpanzee habitat (Grieser Johns 1996, Echroma *et al.* 1997).

Chimpanzees in Uganda

There have been and are several chimpanzee study sites in Uganda. The earliest site was established in the Budongo Forest in the early 1960s (Reynolds & Reynolds 1965a, Reynolds 1967, Albrecht 1976, Goodall 1994b). Albrecht (1976) lists a number of other forests in which chimpanzees occurred in the 1970s in Uganda: Bwindi, Kibale, Kasyoha, Kitomi, Kalinzu, Maramagambo and Ruwenzori, all of which are in the western region of the country close to the border of Zaïre and Rwanda. In 1976 a second study site was opened in the Kibale Forest of Uganda (Ghiglieri 1984, Goodall 1994b). The ecotourism component of the Kibale Forest Project was initiated in July 1991 as a further measure to conserve the chimpanzees and other primate

species in the area and as a revenue-generating sustainable activity with the aim to benefit the local communities surrounding the park (Grieser Johns 1996). Today, the number of wild chimpanzees living in Uganda as estimated by a recent census in 1999/2000 is between 3 000 to 4 000 in 12 separated forest blocks of varying size (Cox pers. comm.⁵).

In summary, the chimpanzee is in imminent danger of extinction in all home range countries. The major threat the species faces is extinction of whole populations by the ever increasing bush meat trade, following the invasion by timber-logging companies, and habitat destruction and fragmentation through human encroachment. Research and/or eco-tourism projects which try to create awareness and sustainable income-generating activities are present in a number of these home range countries. However, the ongoing collection of behavioural data seems to mainly monitor the fast decline of the species, and until now has been unable to counteract this destructive trend in any significant way.

Threats

"All *Pan troglodytes* subspecies are vulnerable to extinction if the factors causing their decline continue to operate at the present pace" (Teleki 1989).

The wild chimpanzee populations still existing face several major threats to their survival (Suzuki 1971, Teleki 1989, 1994, Else 1991, Goodall 1989, 1994b, Bearder 1991, Oates 1995, Hart & Hall 1996, Ammann 1997-1998, Rose 1997-1998, Bermejo 1999):

Deforestation

According to Bearder (1991) even though the tropical forests of the world cover only about 7% of the land surface they contain nearly 50% of the total number of plant and animal species. The destruction of this habitat is pursued at a rate of about 20 to 40 hectare per minute globally (Bearder 1991). The destruction progresses rapidly and, if continued at this speed, there will be only isolated pockets of forest left in the middle of the 21 century (Bearder 1991, Hamilton 1992).

The main reason for this continuing destruction is a constantly progressing human encroachment due to a dramatic and unending increase in human population in the countries that constitute the equatorial forest belt (Teleki 1989, Goodall 1989, 1994b, 1998, Bearder 1991, Hamilton 1992, Oates 1995, Hart & Hall 1996, Bermejo 1999). This constant reduction of habitat

⁵ Cox, D. 2001. Jane Goodall Institute Uganda, Entebbe, Uganda.

leads to an increasing pressure on wild populations that very often respond with a decrease in population density through reduced reproduction (Medley 1993).

The habitat reduction does not occur in a circular way around intact forest habitats but rather in a haphazard way wherever need arises. It therefore also results in increasing fragmentation of the habitat, creating more and more edge-effect zones (Bearder 1991, Else 1991, Tutin & Fernandez 1991, Hamilton 1992, Medley 1993, Goodall 1994b, Oates 1995).

The increasing fragmentation and hence the increasing number of contact zones between forested and deforested areas also lead to an increase in primate-human contacts and interactions. This is disadvantageous to both species: through the close phylogenetic relation between human and non-human primates, and here especially to the chimpanzee (Ruvolo *et al.* 1991, Heltne 1994), both species also are susceptible to a number of each other's diseases and therefore constitute an infection risk to each other (Goodall 1994b, Rose 1997-1998, Gagneux *et al.* 2001).

As proven for HIV, Ebola and possibly other still unknown infectious agents, this increased interaction can be a lethal one for the human primate (Goodall 1994b, Rose 1997-1998, Gagneux *et al.* 2001, PROMED-MAIL 2001a+b, 2002a+b). On the other hand, the exposure, through human contact, to virus and other infectious disease agents to which the immune system of the forest-dwelling great ape is naive, can have disastrous consequences and reduce an entire population to such low numbers that it might be impossible to recover (Teleki 1989, Raub 1992, Goodall 1994b, 1998, Rose 1997-1998).

Another result of this increased interaction and close proximity is the easy accessibility to human food sources by non-human primates. They become pests and start raiding crop fields and human settlements where they sometimes even break into houses to steal food, while at the same time destroying a fair amount of the interior equipment as well (Johns & Skorupa 1987, Else 1991). Needless to say that this unfortunate trait of their non-human relatives does not endear these primates to the human population in their closest proximity. Instead, the latter use a number of strategies, from simple shouting to the use of traps and firearms, in an attempt to rid themselves of their intruders (Else 1991). This hostile attitude makes conservation efforts even more difficult to promote and achieve (Teleki 1989, Else 1991, Goodall 1994b, Rose 1997-1998).

However, well-intentioned and -perceived conservation projects can run the danger of undermining their own cause (Oates 1995). To prevent local communities from exploiting the resources inside the protected areas by trying to increase productivity and the standard of living in border zones around nature reserves and parks, these border zones might actually become 'too attractive' (Oates 1995). Oates (1995) gives an example from the Okomu Forest Reserve in Nigeria where the introduction of a 'development component' into the management of the park reversed the observed trend of population migration from the area. Through increased supply of crop seeds and infrastructure, immigrants from distant parts of the country were attracted to the area. At the same time no stringent measures were taken to enforce the compliance of the ever increasing community with the beforehand established conservation plan and objectives. Instead, the encroachment into the protected park area progressed steadily and led to even further habitat destruction (Oates 1995).

The Bush meat trade

The bush meat trade (Figures 4.2 – 4.5) is an ever increasing threat to chimpanzee and gorilla populations in many of the west and central African countries (Skorupa & Johns 1987, Teleki 1989, Goodall 1989, 1994b, Ammann 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998, Gagneux *et al.* 2001). Together with other forest-dwelling mammals, apes have been hunted for meat in equatorial Africa for millennia in a largely sustainable manner (Kortlandt 1984, Gagneux *et al.* 2001).



Figure 4.2: Bush meat in the forest (Photo: K. Ammann – with kind permission).

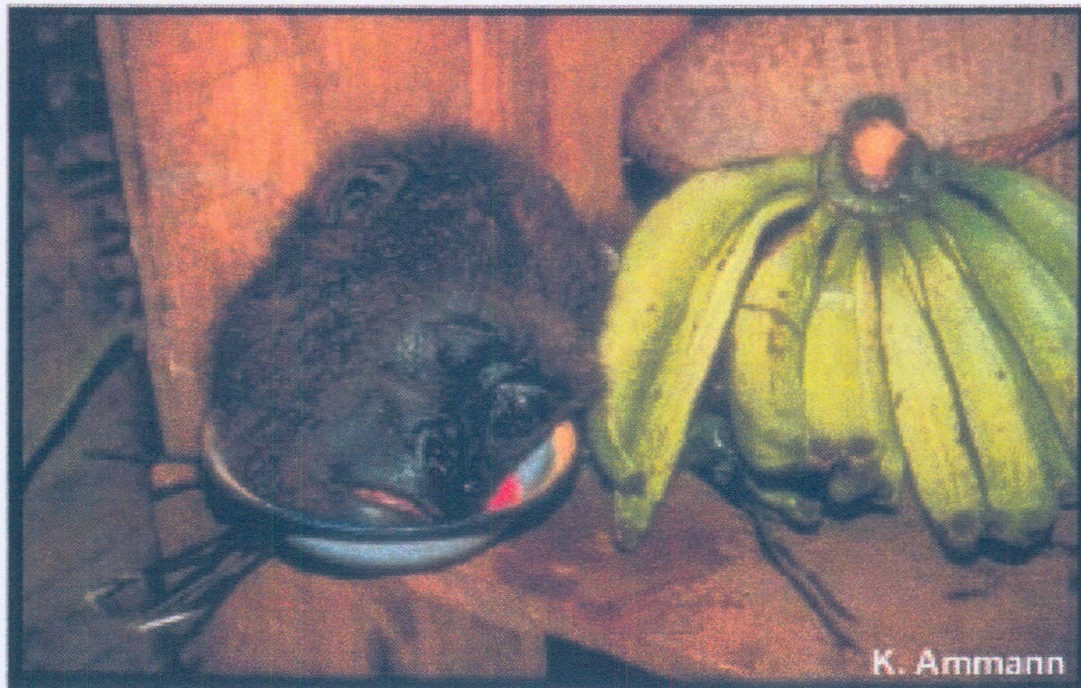


Figure 4.3: Bush meat at home (Photo: K. Ammann – with kind permission).



Figure 4.4: Smoked primate bush meat (Photo: K. Ammann – with kind permission).



Figure 4.5: Bush meat baby (Photo: K. Ammann – with kind permission).

A paramount new threat to the survival of the chimpanzee in the wild is the increasing commercialization of the bush meat trade that makes it unsustainable (Teleki, 1989, Goodall 1994b, 1998, Ammann 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998). This has been caused by the immense increase of commercial logging in a number of African countries inside the tropical forest realm. These logging companies, mainly based in European countries such as France, Germany, Italy, United Kingdom, and more recently also in Asia, open up the forests and bring with them a large number of employees that needs to be fed. The logging companies supply local hunters, very often pygmies, with automatic rifles to ensure hunting success (Teleki 1989, Ammann 1997-1998, Bowen-Jones 1997, Rose 1997-1998).

A newly constructed road system, established by the logging companies, provides easy access to previously inaccessible areas of tropical rain forest habitat. The hunters or, in most cases, their middlemen also use the vehicles of the logging companies to transport large quantities of bush meat to local markets and to the major markets in the urban centres of the west and central African countries (Ammann 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998).

Bush meat constitutes a major protein source in many African countries and the demand is constantly increasing especially in the large urban centres of west and central Africa (Amman 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998). It is this ever increasing urban demand that mainly fuels the bush meat trade. Bush meat attains much higher prices than livestock meat in most of the urban markets, whereas back in the villages this ratio is reversed. Thus, selling in distant urban markets is a very lucrative business which is even extended into neighbouring countries if the road infrastructure and the demand across the border are present (Ammann 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998).

The main targets for bush meat are primates and artiodactyls, especially duikers. Many of the hunted mammals are at risk from the bush meat trade and might well be brought to extinction if the hunting pressure continues or increases in the future (Teleki 1989, Goodall 1994b, 1998, Amman 1997-1998, Bowen-Jones 1997-1998, Rose 1997-1998).

Bowen-Jones (1997-1998) provides the following list of mammals believed to be at present threatened through the bush meat trade (also: APE ALLIANCE 1998):



<i>Cephalophus duiker</i>	Zebra duiker
<i>Cephalophus jentinki</i>	Jentink's duiker
<i>Cephalophus leucogaster</i>	White-bellied duiker
<i>Cephalophus niger</i>	Black duiker
<i>Cephalophus ogilbyi</i>	Ogilby's duiker
<i>Cephalophus sylvicultor</i>	Yellow-backed duiker
<i>Cercopithecus diana</i>	Diana monkey
<i>Cercopithecus erythrogaster</i>	White-throated monkey
<i>Cercopithecus erythrotis</i>	Red-eared monkey
<i>Cercopithecus hamlyni</i>	Owl faced monkey
<i>Cercopithecus preussi</i>	Preuss's monkey
<i>Cercopithecus sclateri</i>	Sclater's monkey
<i>Cercopithecus solatus</i>	Sun tailed monkey
<i>Colobus satanas</i>	Black colobus
<i>Colobus vellerosus</i>	Geoffrey's pied colobus
<i>Gorilla gorilla</i>	Gorilla
<i>Hyemoschus aquaticus</i>	Water chevrotain
<i>Loxodonta africana</i>	Forest elephant
<i>Mandrillus leucophaeus</i>	Drill
<i>Mandrillus spinx</i>	Mandrill
<i>Pan paniscus</i>	Bonobo
<i>Pan troglodytes</i>	Chimpanzee
<i>Panthera pardus</i>	Leopard
<i>Procolobus badius, P. pennantii, P. preussi</i>	Red colobus species
<i>Profelis aurata</i>	Golden cat
<i>Smutsia (Manis) gigantea</i>	Giant pangolin

A sad "by-product" of the bush meat trade is a large number of, especially chimpanzee, orphans. These young animals are too small to be of any value for their meat. Thus, they are often kept as pets in the villages of the hunters or sold as 'living toys' in the logging camps or the big cities, very often to expatriates (Teleki 1989, Goodall 1994b, 1998, Ammann 1997-1998, Bowen-Davies 1997-1998, Rose 1997-1998). Needless to say, not many of them survive this ordeal (Figure 4.5). The few who do eventually end up in cages or are chained in courtyards once they have become too big and strong and are causing too much damage in a 'civilized' home to still be suitable as a 'cute playmate' (Goodall 1994b, 1998, Ammann 1997-1998). Figures 4.2 – 4.5 are examples of the bush meat trade.

The logging of tropical rain forest and the bush meat trade are two unsustainable practices that will eventually lead to the destruction of a huge area with an exceptionally high biodiversity. Ammann (1997-1998) summarizes the prevailing attitude of the people involved in the trade as follows: "Increasing demand and decreasing supply will inevitably result in prices going up. With a limited resource, this will go on until the supply is exhausted, which, according to a Polish missionary, will elicit the response: » Why has God done that to us? «" (Ammann 1997-1998).

Chimpanzee trade

Despite a CITES (Convention on International Trade in Endangered Species of Fauna and Flora) agreement which has been signed by many of the African countries, a vast trade in wild chimpanzees is still ongoing, mainly providing young chimpanzees to laboratories in the United States and as pets or for the entertainment industry all over the world (Borner 1985, Carter 1988, Teleki 1989, Goodall 1998). Many of these chimpanzees are and have been taken from West African countries which explains the low number of *Pan troglodytes verus* in the wild and their exceptionally high abundance in many laboratories mainly in the United States and some of the European and Asian countries (Carter 1988, Teleki 1989).

It is estimated, that on average ten adult chimpanzees are killed when trying to obtain one young chimpanzee from a group of wild chimpanzees. Young chimpanzees are mainly taken while under the age of two years. During this time they still cling to their mother, who has to be shot to seize her infant. Adult male chimpanzees as well as the whole group often defend the dead mother and her infant and have to be shot as well to gain safe access to the youngster (Hladik 1974, Teleki 1989, Goodall 1998).

Teleki (1989) reports that due to the horrendous transport conditions and the appalling care the

young chimpanzees receive on their very long journeys, only about one in five infants reach their new destinations alive. He calculates that sometimes as many as 29 chimpanzees are killed for one live infant chimpanzee arriving at his captive destination (Teleki 1989).

This trade in young chimpanzees has reduced the viable populations in the wild considerably and may push chimpanzees even further towards their extinction, since "time spans measured in decades, not in months or years, are needed for chimpanzee populations to recover once stability is lost" (Teleki *et al.* 1976 in Teleki 1989).

CHIMPANZEES IN CAPTIVITY

"In the milieu of captivity, the most important factor is man; apart from his immediate presence, the whole environment of the captive animal is as it were impregnated with man. Under such circumstances, the most important behavior pattern in freedom, flight from man, the enemy, becomes meaningless... The main problem set the animal in the reconstruction of its subjective world to suit captive conditions is to fit man into the new set of circumstances." (H. Hediger 1950)

"Island Chimpanzees"

Wilson & Elicker (1976) define the different environmental categories in which chimpanzees live, or are kept and in which they are studied:

- | | |
|---------------------------------|---|
| <i>Wild state:</i> | Populations occurring within their natural range and foraging their habitat for all of their food (e.g. Mt. Assirik, Senegal). |
| <i>Semi-wild state:</i> | Populations occurring within their natural range which are also partially provisioned (e.g. Gombe National Park, Tanzania). |
| <i>Free-ranging state:</i> | Groups of primates released outside [or inside] their natural habitat into physically isolated areas where indigenous fauna and flora provide part of their food, and which are also provisioned (e.g. Ipassa, Gabon; Ngamba Island, Uganda). |
| <i>Semi-free-ranging state:</i> | Groups of primates [confined] to large outdoor man-made enclosures (e.g. Arnhem Zoo). |
| <i>Caged state:</i> | Individuals or small groups housed entirely indoors. |

“Island chimpanzees”, like the chimpanzees kept on Ngamba Island, can be considered as being *free-ranging*, even if they have the choice to retreat to their enclosure during night time.

There have been a number of projects where chimpanzees were released on islands either to *reintroduce* them into the wild or to keep them in an environment more suited to their needs for the purpose of establishing a breeding colony (Wilson & Elicker 1976, Pfeiffer & Koebner 1978, Maple 1979, Borner 1985, Carter 1988, Hannah & McGrew 1991).

According to Hannah & McGrew (1991) *rehabilitation* covers several release procedures, namely:

- Release:* To set free captives, often with little or no follow-up of their fate.
- Repatriation:* Animals are returned to the country of origin, usually from temperate climates to more hospitable tropical ones.
- Translocation:* A shift from one wild site to another, with minimal time spent in between, in captivity. By definition, these are wild-born individuals, unlikely to acquire behavioural abnormalities in short-term human contact.
- Reintroduction:* A term frequently used in the general context of ‘restoration’.
- Rehabilitation:* Used in the strict sense of training behavioural inadequate individuals in skills which allow them to survive with greater independence.

Figure 4.6 lists several island rehabilitation projects and shows the respective densities of chimpanzees in the areas where they have been released, expressed as the number of chimpanzees per km².

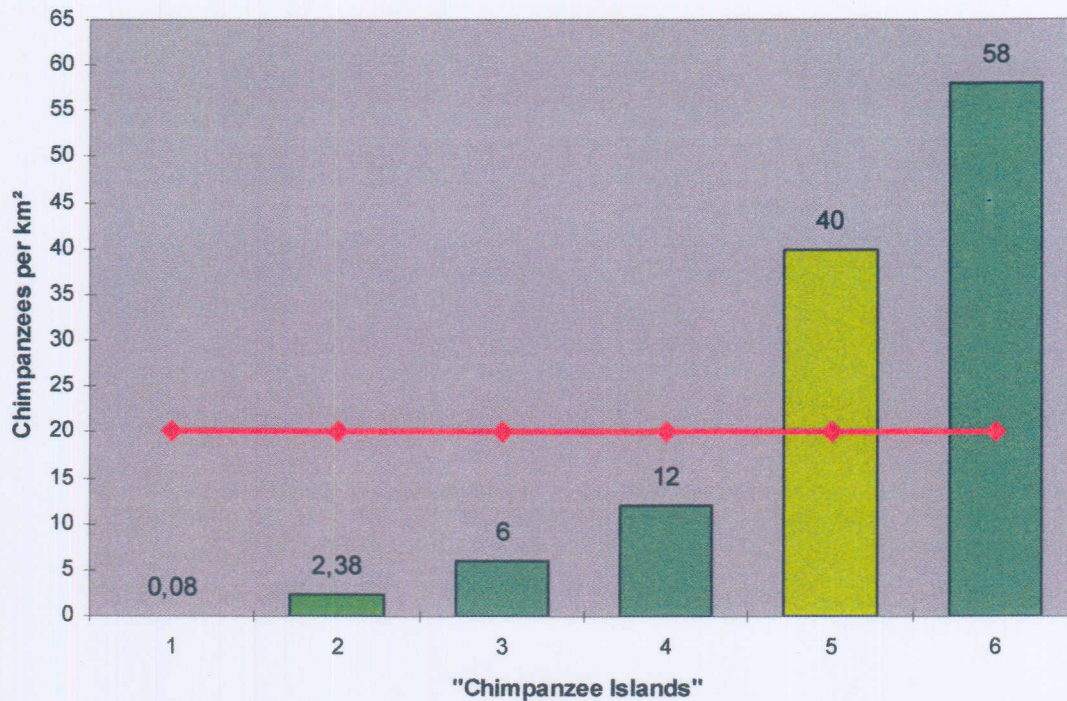


Figure 4.6: Chimpanzee densities in different Island habitats (all densities are given in: number of chimpanzees per square kilometre).

Key:

1. Rubondo Island, Lake Victoria, Tanzania: area: 240 km², number of chimpanzees: 20 (Borner 1985).
 2. Average density of chimpanzees in the wild in a tropical rain forest habitat (Ghiglieri 1984).
 3. Baboon Island, Gambia River, The Gambia: area: 490 ha, number of chimpanzees: 30 (Carter 1988).
 4. Ipassa, near Makokou, Gabon: area: 65 ha, number of chimpanzees: 8 (Hladik 1973, 1974).
 5. Ngamba Island, Lake Victoria, Uganda: area: 40 ha, number of chimpanzees: 16 (this study).
 6. Island A + B, Little Bassa River, Liberia: area 85 ha, number of chimpanzees: 58 (Hannah & McGrew 1991)
- Red line = Estimate by Jenkins (pers. comm.): 5 ha per chimpanzee for self sustainability.

The first project that released chimpanzees onto an island was the rehabilitation of chimpanzees onto Rubondo Island, Lake Victoria, Tanzania. This project was promoted by the Frankfurt Zoological Society and involved the release of 17 chimpanzees between 1966 and 1969. These animals had all been captured in the wild, then kept in several European zoos for different periods of time and eventually released into the forested Rubondo Island National Park. After two months, supplementary feeding was stopped. In 1985 it was estimated that ≥ 20 chimpanzees lived and successfully reproduced on the island (Borner 1985, Hannah & McGrew 1991). The density is about 0.08 chimpanzees per km^2 and is thus still below the mean density of 0.1 chimpanzee per km^2 given by Teleki (1989) for the density of wild populations in a savanna habitat. The *rehabilitation* of the Rubondo Island chimpanzees is an example for a *release* after *Repatriation* as defined by Hannah & McGrew (1991).

From 1968 to 1970 altogether eight chimpanzees were rehabilitated on the 'Ile aux Singes' Ipassa, in the Ivindo River, close to Makokou, Gabon. All individuals had spent a certain time of their life in a laboratory and were then released, with the original aim of reproducing and thus supplying new chimpanzees for research purposes on location (Hladik 1973, 1974, Hannah & McGrew 1991). The island has an area of 65 hectares and the density of the eight released chimpanzees thus equalled 12 chimpanzees per km^2 . Thus 150 times that of the chimpanzees on Rubondo Island and about 40 times higher than the mean density of 0.3 chimpanzees per km^2 given by Teleki (1989) for chimpanzee densities in a tropical rain forest habitat, like the one found on Ipassa. However, these chimpanzees were provisioned with bananas to supplement the available food resources on the island (Hladik 1973, 1974). The chimpanzees eventually discovered that they could leave the island during low tide and wade back and forth to the mainland. Eventually, six of the eight were recaptured during one of their visits and brought back to the laboratory, while the remaining two escaped (Hannah & McGrew 1991).

Carter (1988) describes the *repatriation* of a number of chimpanzees from the United States to The Gambia during the late seventies. A number of locally confiscated chimpanzees were added to this group. Eventually, in late 1985, a second group was added and both groups together were released on Baboon Island in the Gambia River (Carter 1988, Hannah & McGrew 1991). The island covers an area of 490 ha and at present contains a group of over 30 chimpanzees who are provided with supplementary food. The chimpanzee density on Baboon Island is about 6 chimpanzees per km^2 (Carter 1988, Hannah & McGrew 1991).

Jenkins (pers. comm.⁶) estimates that for the self-sustainable survival of free-ranging chimpanzees in a tropical forest habitat at least 4 to 5 ha need to be allocated to every single chimpanzee to avoid a permanent destruction of the environment. This translates in a density of 20 chimpanzees per km², which is nearly 67 times higher than the mean number given by Teleki (1989) for wild populations.

On Ngamba Island, Lake Victoria, Uganda, the number of adult chimpanzees who are *free-ranging* in the forest during the day, is 16. To facilitate comparison between the island sites the number of juveniles is not considered since they only spend several hours a week inside the forest area. However, the damage caused by those youngsters is quite remarkable.

With a density of 40 chimpanzees per km², Ngamba Island has double the maximum density suggested for self-sustainable capacity of the area, as estimated by Jenkins. However, the Ngamba chimpanzees are provided with all the food they need and thus have the fruit and non-fruit food available in their forest habitat as 'extras'. The density of the Ngamba Island chimpanzees is about 133 times higher than the mean chimpanzee density as given by Teleki (1989) for a rain forest habitat.

There is a group of two islands (A + B) in Little Bassa River, Liberia, linked by mangrove swamps, which has an even higher density of chimpanzees (Hannah & McGrew 1991). These chimpanzees had been released from the local Vilab research laboratory (which is part of the Laboratory of Virology of the New York Blood Centre) and were supposed to be *reintroduced* into the wild after an adaptation to their natural habitat during their *release* period on Island A + B. With 68 chimpanzees per km² the density is 1.7 times higher than the density of adult chimpanzees on Ngamba Island (Hannah & McGrew 1991).

The most extreme example of chimpanzee density on an island rehabilitation site comes from Florida. Pfeiffer & Koebner (1978) released previously single-caged chimpanzees, after a short introduction phase, onto an 0.13 hectare island (Pfeiffer & Koebner 1978, Hannah & McGrew 1991). Altogether, eight chimpanzees originating from LEMSIP (The Laboratory for Experimental Medicine and Surgery in Primates, New York University School of Medicine) were brought to the island belonging to Lion Country Safari, West Palm Beach, Florida, U.S.A. (Pfeiffer & Koebner 1978). The chimpanzees were released on the island to study the social integration of previously single-caged chimpanzees and focusing especially on the alteration and persistence of pathological behaviour. The chimpanzee density on the island can be projected as being

⁶ Jenkins, P. 2001. *Pandrillus*, Calabar, Nigeria.

equal to 6 154 chimpanzees per km². Thus, the laconic remark of the authors that “the animals first destroyed the enclosure and most of the trees” does not come as a surprise (Pfeiffer & Koebner 1978). Furthermore, a picture showing part of the island also shows “the trees stripped of bark and most of their branches” (Pfeiffer & Koebner 1978).

The Yerkes Regional Primate Research Centre released laboratory chimpanzees on Bear Island, part of Ossabaw Island, Georgia, U.S.A., from June 1972 onwards (Wilson & Elicker 1976). Since reports vary regarding the size of the area available to the chimpanzees no comparisons can be made. Although some of the chimpanzees had died, the authors were still enthusiastic about the progress and outcome of their release operation in 1976 (Wilson & Elicker 1976). Maple (1979) reports that after five years and after a number of more animals had died, the chimpanzees were again removed from the island. The decision was partly made as a result of the constant danger of the animals drowning and the difficulty of maintaining the chimpanzees under absentee management conditions (Maple 1979).

Maple (1979) summarizes the major problem of island facilities for released chimpanzees as follows: “Another problem with islands is that unless they are quite large, the inhabitants will soon eat their way out of house and home. Therefore, it is often necessary to build artificial structures which provide shade and refuge should foliage be depleted”.

Enclosure design

“To acknowledge that a captive primate is still a wild primate is the first and necessary step in providing for its needs” (Maple 1979).

Maple (1979) thus states that it is not enough to consider ape-keeping as being successful if *bearing and rearing of offspring* has been fulfilled. This author considers the animal adequately housed and / or reared only if the captive animal is free of the bizarre behaviours of “stereotyped motor acts, autoerotic and autoagonistic behaviors” (Maple 1979).

An appropriate enclosure design is of utmost importance especially in zoos where the space of the captive chimpanzees is normally very restricted. It is compulsory that a stimulating environment is provided for all species in zoos (Latinen 1989), including “intellectual employment” for the inquisitive-minded chimpanzee (Kortlandt 1960/61). In short, outdoor and indoor facilities must be provided with appropriate “furniture” to ensure increased environmental diversity as well as physical and psychological stimulation (Kortlandt 1960/61, Reynolds &

Reynolds 1965a, Van Hooff 1973, Maple 1979, Latinen 1989, Coe 1992, Gold 1992).

The Arnhem Zoo is regarded as a prime example of provision of an adequate environment for its captive chimpanzees (Van Hooff 1973, Gold 1992). There is an outdoor and an indoor enclosure and the chimpanzees can choose freely where they want to pass their time; only in winter are they confined to the indoor enclosure alone (Van Hooff 1973, Gold 1992). That allows the chimpanzees to choose the temperature they feel most comfortable with and to find shelter and protection from the view of too curious visitors whenever they so desire (Kortlandt 1960/61, Wrangham 1992). A ditch separates the outdoor enclosure and chimpanzee forest from the public, thus providing a good view for the public undisturbed by an ugly fence construction (Van Hooff 1973).

An important consideration for enclosure design, indoors and outdoors, is to provide escape routes for young or subordinate individuals that enable them to escape attacks, and thus injury or accidental death, from superior adult chimpanzees (Kortlandt 1960/61, Van Hooff 1973).

Chimpanzees should never be kept alone and even in zoos, should be kept in groups, whenever possible (Kortlandt 1960/61, Reynolds & Reynolds 1965a, Maple 1979, Wrangham 1992).

Behavioural Enrichment

“Yet what is “freedom” but the relative number of choices available” (Coe 1992).

Chimpanzees in captivity often develop stereotypic or other atypical or undesirable behaviours such as regurgitation and reingestion, coprophagy, increased aggression, frequent throwing of sticks, stones or faeces, rocking, and self-mutilation (Reynolds & Reynolds 1965a, Van Hooff 1973, Maple 1979, de Waal 1994, Baker & Easley 1996). It is therefore generally agreed upon that as much natural behaviour as possible should be encouraged in all non-wild and non-semi-wild chimpanzees (Kortlandt 1960/61, Reynolds & Reynolds 1965a, Van Hooff 1973, Maple 1979, Redshaw & Mallinson 1991, Coe 1992, Gold 1992, de Waal 1994, Cox *et al.* 2000).

Behavioural enrichment can have many hues and colours, e.g. provision of natural and artificial climbing structures, including ropes and chains, tunnels, large rocks as outlooks, provision of old tyres and cut-off branches or straw as nesting material, provision of clothes and painting materials, hiding of food samples inside the enclosure, including the application of a colour code to indicate favourable or less-favourable food items, flexible feeding schedules and a frequent

change of at least a certain number of provided toys to prevent boredom (Kortlandt 1960/61, Reynolds & Reynolds 1965a, Van Hooff 1973, Maple 1979, Gust 1989, Redshaw & Mallinson 1991, Coe 1992, Gold 1992, Wrangham 1992, de Waal 1994, Bloomsmith & Lambeth 1995, Fouts & Tukul Mills 1997, Cox *et al.* 2000).

How these considerations might be used to improve the well-being of free-ranging chimpanzees in a sanctuary environment while at the same time reducing the destruction of the natural habitat will be evaluated in detail in the discussion (Chapter 7).

CHIMPANZEE HABITAT

Kortlandt (1984) and Teleki (1989) provide maps giving the historical distribution of the two *Pan* species. When comparing these distribution ranges with White's (1983) classification of the vegetation of Africa it becomes obvious that chimpanzees are adapted to survival in a wide variety of habitats. "Chimpanzees utilize dry savannah-woodlands, mosaic grassland forests, and humid canopy rain forests, and live from sea level to at least 3 000 m elevation; however, the availability of permanent sources of surface water may be a key factor limiting the chimpanzees at the fringes of their geographical range" (Teleki 1989).

The centre of the chimpanzee's distribution range consists of White's (1983) "I. Guineo-Congolian regional centre of endemism". This is bordered to the south by the "X. Guinea-Congolian/Zambeian regional transition zone", to the north by the "XI. Guineo-Congolian/Sudanian regional transition zone" and to the east by the "XII. Lake Victoria regional mosaic". The marginal habitats of the chimpanzee distribution range reach into the "II. Zambeian regional centre of endemism" towards the south and into the "III. Sudanian centre of endemism" towards the north and north-west (White 1983, Kortlandt 1984, Teleki 1989).

According to Kortlandt (1984) the northern boundary of viable chimpanzee habitat is determined by the reduction in floristic richness, while the south-eastern boundary is determined by general climatic and ecological conditions.

The classification of vegetation types (originally) inhabited by chimpanzees varies more or less from author to author: Reynolds (1967) mentions habitat types such as 'tropical rain forest', 'montane forest' and 'tropical woodland', while Suzuki (1969) refers to the area where he studied chimpanzees in western Tanzania as 'savanna woodland' or 'miombo woodland'. Hladik (1974) describes the habitat of Mpassa as "la grande forêt dense sempervirente", i.e. dense, evergreen

(rain) forest. Collins and McGrew (1988) compare three different habitats on the eastern shore of Lake Tanganyika: namely Bilenge, "mostly open woodland of *Brachystegia*, with relatively little riverine forest"; Kasoje, "predominantly forested with limited open vegetation"; both at Mahale Mountains and Gombe, "less open woodland, but extensive thicket woodland (or semi deciduous forest)". They ascribe these differences mainly to the differences in precipitation at the two locations. While these authors emphasise the difference in vegetation structure between the Mahale Mountains and the Gombe region, Nishida *et al.* (1983) consider these two habitats to be similar with a more extensive floral diversity at Mahale than at Gombe, due to higher rainfall at the former location.

McGrew *et al.* (1981) and Baldwin *et al.* (1982) differentiate five different vegetation types around Mt Assirik in the Park National du Niokolo-Koba, Senegal. This area is considered to be the "north western edge of the species distribution" (McGrew 1989). The authors list the following chimpanzee habitats with their associated vegetation, (1) gallery forest: tropical (or subtropical) semideciduous lowland forest, (2) woodland: drought-deciduous lowland woodland, (3) bamboo: flat-leaved savannah with isolated palms and deciduous trees, (4) grassland: narrow-leaved savanna with isolated palms and deciduous trees, and (5) plateau: narrow-leaved savannah with isolated deciduous shrubs (McGrew *et al.* 1981, Baldwin *et al.* 1982).

Bermejo (1999) distinguishes four major vegetation types as chimpanzee habitat in the Odzala National Park, northern Congo, namely (1) primary forest, on *terra firma* and inundated soils, (2) Marantaceae forest, i.e. evergreen forest with a dense under storey of Marantaceae species, (3) clearings, and (4) savannas. She subdivides the two forest types, i.e. Marantaceae forest and closed primary forest, according to their underlying soil conditions in (1) *terra firma* forest and (2) riparian forest, i.e. thicket, dense inundated and swamp forest (Bermejo 1999).

Eventually, White (1983) in his book "The vegetation of Africa" divides the whole of Africa into 21 different, so-called "phytochoria" or phytogeographic areas and defines the major vegetation types present. In the six phytochoria (I, II, III, X, XI, XII) which constitute viable chimpanzee habitat, the following vegetation types are represented (White 1983):

1. *Forest*: A continuous stand of trees at least 10 m tall, their crowns interlocking.
2. *Woodland*: An open stand of trees at least 8 m tall with a canopy cover of 40 per cent or more. The field layer is usually dominated by grasses.

3. *Bushland*: An open stand of bushes usually between 3 and 7 m tall with a canopy cover of 40 per cent or more.
4. *Thicket*: A closed stand of bushes and climbers usually between 3 and 7 m tall.
5. *Grassland*: Land covered with grasses and other herbs, either without woody plants or the latter not covering more than 10 per cent of the ground.
6. *Wooded grassland*: Land covered with grasses and other herbs, with woody plants covering between 10 and 40 per cent of the ground.
7. *Scrub forest*: Intermediate between forest and bushland or thicket.
8. *Transition woodland*: Intermediate between forest and woodland.
9. *Scrub woodland*: Stunted woodland less than 8 m tall or vegetation intermediate between woodland and bushland.

The tropical rain forest habitat

“Evergreen, hygrophilous in character, at least 30 m high, but usually much taller, rich in thick-stemmed lianes and in woody as well as herbaceous epiphytes” (Schimper 1903 in Richards 1966). In contrast to this description of the primary tropical rain forest vegetation Richards (1966) defines a *typical secondary rain forest* as “the earlier seral stages found on areas which have been cultivated or exploited for timber, but not subsequently grazed or burnt.”

The general characteristics of tropical rain forests have already been described in Chapter 3. Today the prime tropical rain forest habitat of the chimpanzee is one faced by steady decline through (1) increasing human encroachment and (2) increasing commercial logging of timber (Brown 1981).

Logging and natural tree mortality

Figure 4.7 shows a train loaded with logged timber and the destruction caused by the infrastructure necessary for economic timber exploitation.



Figure 4.7: Train transporting timber logged in an African tropical rain forest.

General considerations

Myers (1980) believes that timber exploitation of tropical forest *per se* could be causing the effective conversion of somewhere between 17 700 and 29 000 km² of primary forest in the moist tropics each year.

Brown (1981) develops several suggestions for the protection of the remaining tropical forest areas. His underlying principle is to preserve as large an area as possible (Brown 1981). Brown (1981) considers the remaining patches of lowland and montane forest in Africa to follow *island biogeography theory* as far as the rate of species loss or turnover is concerned. Diamond (1981) differentiates between montane forest islands and lowland forest islands. He considers the former as *oceanic islands*, since they originally received their biota through long-distance dispersal and now show a species turnover around a constant equilibrium (Diamond 1981). The latter should be considered as *land-bridge islands*, formed by the continuous reduction of a formerly much larger area, which will experience a continued reduction of species numbers through decreased size until a new sustainable species density for the remaining area is reached (Diamond 1981). The most important feature of an oceanic island (montane or in the sea) is its proximity to a species source area to ensure constant influx of new species (Diamond 1981).

According to Brown (1981) there should be a number of measures and approaches to save the remaining forest habitat from further human encroachment and subsequent soil erosion:

1. Soil conservation
2. Intensification of agricultural practice to increase yield
3. Plantations which promote the cultivation of cash crops.

The latter point brings with it a number of risks: If a high-priced cash crop production is successful there will be the temptation to extend the cash crop area by reducing the protected forest habitat even further. These plantations often depend on a large amount of fire wood and thus the forest might have to give way to a further plantation of fast-growing tree species (Brown 1981). On the other hand, plantations, especially forest or tea plantations can be used as buffer zones between subsistence farming agriculture and its accompanying human encroachment and the conservation area. They can also act as fire breaks and livestock barriers (Brown 1981).

Brown's (1981) overall advice and conclusion is "to leave the [conservation] area strictly alone until the facts are better understood".

Bada (1989) fitted the 'Chapman-Richard Model' for the prediction of forest growth and yields to growth data of some secondary tree species in a mixed tropical forest.

His modified equation is as follows:

$$B^* = [n/k - C.e^{-(1-m)Kt}]^{1/(1-m)}...$$

With B^* = the predicted basal area [of a specific tree species] at a given time
 "t" = the initial time (i.e. from the time of girth measurement)
 e = exponentiation constant (2.71828)
 K, m, n = growth parameters best determined by the maximum likelihood method.

The growth variable "C" is derived as: $C = n/k - B^{(1-m)}$

With B = initial basal area.

This equation was adapted to four secondary tree species for which long term data were available. No significant differences were found between the predicted and the actual basal area. Although the author also found, that the degree of accuracy of stand basal area prediction with the model appeared to decrease with time, this decrease was not statistically significant (Bada 1989).

Riddoch *et al.* (1991) postulate that the successional status of a species is determined by the ability of this species' seedlings to exploit the light environment and nutrient supply which characterize a particular stage of canopy development (Riddoch *et al.* 1991). *Pioneer species* are those species with an enhanced capacity to utilize the high light environment associated with clearings or gaps in the canopy. Whereas *climax species* are those species which survive as saplings in deep shade (Riddoch *et al.* 1991). Although it was demonstrated that the respiration rates of shade-acclimated leaves of climax species were low compared to those of 'sun leaves' of pioneer species, the differences between the two species types were not such that a clear-cut prediction between their growth patterns and their exposure to light could be made (Riddoch *et al.* 1991). Light is therefore not the only variable of importance in determining seedling growth and successional status of a species. Other factors, such as humidity, temperature, and CO₂ also influence seedling growth of pioneer and climax species (Riddoch *et al.* 1991).

Pannell (1989) draws the attention towards a major problem caused by the increasing destruction of viable tropical forest habitat. Most of the rain forest tree species rely on animals for

pollination and seed dispersal. As a result of the widespread destruction of the rain forest the presence of these animal seed dispersers can no longer be guaranteed (Martínez-Ramos & Alvarez-Buylla 1986, Howe 1989, Pannell 1989, White 1994a, Hashimoto 1995).

The continued production of timber in the tropical rain forest belt depends on natural regeneration after logging. Representative and viable areas of tropical rain forest should therefore be retained within timber production areas to perpetuate viable populations of the plant and animal life typical of the local forest habitat (Pannell 1989). These areas should be totally and permanently protected from logging, burning, and other human disturbances and suitable breeding and roosting sites must be available. The protected animal populations furthermore should be large enough for a breeding population to persist after an attack by predators, pests or diseases (Pannall 1989).

Johns & Skorupa (1987) evaluated the response of primates to habitat disturbance by selective logging in a rain forest habitat. Selective logging here means the clearing of up to 10% of the trees from an area of forest while the residual stand is left to regenerate (Johns & Skorupa 1987). The authors found that some primate species can possibly survive alongside logging. In general body size and frugivory of a certain primate species explain 44% of the variation in species responses to moderate habitat disturbances (Johns & Skorupa 1987). Within any specific dietary strategy, large-bodied species are generally more sensitive to a forest disturbance than smaller-bodied species. When the authors controlled for the effects of dietetic diversity and body mass they found that diet type is very strongly correlated with survival ratios, being strongly positive for folivorous and strongly negative for frugivorous primate species (Johns & Skorupa 1987). The authors conclude that generally "*large-bodied frugivores* are the class of primates most vulnerable to habitat disturbance", which thus also and especially affects chimpanzees and their survival in disturbed habitats (Johns & Skorupa 1987).

Rain forest management in Uganda

Ugandan rain forests occur in three ecological zones (Table 4.1) (Harcourt 1992).



Table 4.1: *Estimates of forest extent in Uganda (following Harcourt 1992)*

Rain forests	Area [km ²]	% of land area
Lowland	6 318	3.2
Montane	2 212	1.1
Swamp	265	0.1
<i>Total</i>	<i>8 795</i>	<i>4.4</i>

Since 1929 the Ugandan government has been applying a forestry policy which is briefly outlined below (Harcourt 1992):

1929 – 1959 *Polycyclic felling system* – trees exceeding a minimum girth were harvested about every 30 years on a 60 to 90 year rotation.

No felling without prior systematic stock mapping by the Forestry Department was allowed. Only marked trees could be cut, while minimum girth limits were endorsed. Tree plantations were established for enrichment planting after timber harvest. Arborescence treatment was applied to remove undesirable trees. Since this system interfered relatively little with the natural state of the forest regeneration was mainly natural rather than by enrichment planting.

1960 – 1970 *Monocyclic felling system* – replacement of the polycyclic system.

No lower limit on the size of the trees cut. This system was a far more deleterious impact on forest wildlife and ecology of the forest than the polycyclic system.

1971 – 1986 Under Amin's regime – general break down of forest control.

Greater emphasis was put on short-term profit from timber extraction while Protective forestry was ignored. About 100 km² of forest were lost every year from 1981 to 1985.

1987 - Present Revised forest policy

Management of the forest to optimise economic and environmental benefits by ensuring that conversion of the forest resources to timber, charcoal and the like is carried out efficiently; that the forest estate is protected against encroachment, illegal tree cutting, fires, diseases and pests; and that sustainable methods are used for harvesting.

This policy might be difficult to put into practice. Ninety to 95 per cent of the wood consumed in the country is for fuel, most of it is even till today still coming from public land outside the forest reserves such as fuel wood plantations, small remnant patches of natural forest and woodland (Harcourt 1992). But Uganda has a high population growth rate of more than 3 per cent per year with the population having doubled since the 1960s (Harcourt 1992). The constant influx of immigrants from overcrowded districts will make it more and more difficult to sustainably protect the remaining Forest Reserves in Uganda (Harcourt 1992).

“No attention is given to the complex and fragile nature of the rain forest which has taken thousands of years to evolve to its present state and within our lifetime could be totally

devastated by man“ (Struhsaker 1981).

Struhsaker (1981, 1987) is concerned about primate and forest conservation in Uganda. He found that the number of ape and monkey species in any medium to low altitude rain forest was dependent on the following major factors: (1) floral diversity, (2) proximity to upper Pleistocene forest refugia, and (3) the size of the forest (Struhsaker 1981, 1987).

Most non-human primates are forest-adapted. When evaluating primate species numbers in Uganda, Struhsaker (1981) found that the distance from Pleistocene forest refugia was inversely related to the number of anthropoid species present in the remaining forest habitats. This strongly supports the classification of those remaining forest habitats as *land-bridge islands* (Diamond 1981, Struhsaker 1981). Furthermore, Struhsaker (1981) established that the species diversity among these non-human primates is directly related to tree-species diversity and the diversity of anthropoid species depends on floristic diversity. It follows that protected forest habitats should be as large as possible to ensure high tree species richness to sustain a maximum species diversity of anthropoids (Struhsaker 1981).

Struhsaker (1981) gives the example of Kibale Forest Reserve which is subject to selective felling on a polycyclic basis, followed by 'refining', i.e. the poisoning of undesirable trees. Often, these trees constitute an important part of the diet of primates inhabiting the forest, such as fig species for chimpanzees (Albrecht 1976). Struhsaker concludes that even selective logging has an adverse effect on most, if not all, primate species in the Kibale Forest Reserve. This author thus contradicts Harcourt (1992) who found, that a lightly logged forest will support primate populations in more or less the same way as an unlogged forest. Bowen-Jones (1997-1998) could find no example where selective logging has been practiced successfully alongside efforts to conserve floral and faunal species in the same habitat. The issue of selective logging and its effects therefore seems to be highly disputed and possibly to a large extent also dependent on forest type and tree-selection method regarding its impact on the forest habitat.

Struhsaker (1981) concludes his discussion with the following statement: "Conservation of primates essentially deals with the conservation of their habitat, the forest ecosystem... Clearly, the most important step to conserving rain forests and primates (including our own species) is to control this potentially disastrous growth rate of the human population". Struhsaker (1987) underlines his view when stating that deforestation significantly exceeds afforestation.

The author furthermore stresses the fact that tropical rain forests additionally possess a high

value by constituting “genetic storehouses“. Struhsaker (1987) gives the examples of:

- (1) *Foods* derived from tropical forests, such as coffee (*Coffea canephora*),
- (2) *Medicines* derived from tropical forests, such as the use of traditional medicinal plants in eastern Africa and of plant-derived drugs and pharmaceuticals which were valued at US\$ 16 billion in 1980 in the USA alone,
- (3) *Natural pest control*, in the way that many natural predators of insect pests and valuable pesticides derived from forest plants might be used commercially and successfully in the biological control of agricultural pests, such as *Balanites wilsonia*, the fruit of which kills the snails carrying Bilharzia and water fleas transmitting guinea worms, and
- (4) *Tree plantations and ornamentals* created by non-destructive harvesting of seeds to establish woodlots of indigenous tree species for domestic consumption, and of ornamental plants for export.

Skorupa & Kasenene (1984) use the rate of natural tree falls in Kibale Forest to develop a guideline for tropical forest management. The authors compared three forest blocks 12 years after logging had taken place at different intensities. The control area, K-30, had a size of about 300 ha of relatively undisturbed mature forest. In the past only about 3 to 4 stems per km² had been felled by pit-sawyers. Since 1970 the area had been protected from any interference and was thus used as ‘undisturbed control forest’ by Skorupa & Kasenene (1984) for their study. The second compartment, K-14, was about 390 ha in size and had been subjected to selective logging averaging about 14 m³ per ha between May and December 1969. This plot was considered as being ‘moderately disturbed’ (Skorupa & Kasenene 1984). The third compartment, K-15, about 360 ha in size, had also been selectively logged between September 1968 and April 1969, averaging 21 m³ per ha. This plot was considered to be heavily disturbed (Skorupa & Kasenene 1984).

The authors determined the mean annual rate of tree fall to be 1.4% for K-30, 1.3% for K-14, and 6.2% for K-15. Compared to data from mature forests in Malaysia, Skorupa & Kasenene (1984) consider a tree fall rate of 1.3% or 1.4 % as a natural tree fall rate. Whereas the tree fall rate of the heavily disturbed plot K-15 is significantly higher. Since the last logging occurred about 12 years ago in K-15, Skorupa & Kasenene (1984) consider most of the fallen trees in K-15 to have been healthy individuals that were simply uprooted by wind. They attribute the high tree fall rate

to changes in forest structure that affect factors such as aerodynamic roughness, windbreak protection provided by neighbouring trees, and soil cohesion (Fons 1940, Skorupa & Kasenene 1984). The authors conclude that light to moderate logging rated as about 25% destruction, disrupted the regulatory process of natural tree fall only temporarily, if at all. Heavy disturbance or logging seriously disrupted the rate of natural tree fall, which is an integral component of any forest's dynamic balance, in Kibale Forest (Skorupa & Kasenene 1984). The authors consider a tree fall rate of up to 2.3% as normal and calculate an upper limit for forest destruction through logging in Kibale Forest as 35% (Skorupa & Kasenene 1984). They furthermore advise that mechanised selective timber harvesting in Kibale Forest may not be a sustainable means of timber exploitation, especially because of the high amount of incidental, i.e. non-marketable, destruction associated with logging (Skorupa & Kasenene 1984). According to these authors, pit-sawing greatly reduces this incidental destruction and might allow a non-disruptive level of destruction and timber exploitation for Kibale Forest (Skorupa & Kasenene 1984).

White (1994b) cites an example of commercial mechanised selective logging in the lowland rain forest of the Lopé Reserve, Gabon. The extraction rate was two trees per hectare, but incidental damage and cutting of trees that were not extracted, resulted in a mean loss of 2.8 trees ≥ 700 mm dbh (diameter at breast height) per hectare (White 1994b). Altogether, about 20% of trees > 700 mm dbh were lost during logging. Most of those were cut and extracted. The overall damage levels (to all trees) were between about 10 to 13%, while 28.3% of ground vegetation was altered and almost half of the canopy cover was disturbed (White 1994b). Compared to other African countries, White (1994b) still considers this level of damage caused by logging to be low in Gabon. Values for incidental damage in Nigerian rain forests are 44%, in Kibale Forest, Uganda, it is 25% in lightly logged and 50% in heavily logged forests, and the total damage per area in Bia South, Ghana, is estimated at 20% to 30% (White 1994b).

Intensive hunting normally occurs alongside most logging operations and indirectly affects forest dynamics. Hunting reduces primate numbers and since these primates also function as seed dispersers for a large number of trees in tropical rain forests, their decline might have an additional negative impact on forest regeneration after logging operations. Thus, even if sustainable timber logging theoretically seems possible it might be unsuccessful due to the secondary negative effects of the logging operations on the seed-dispersing fauna in tropical rain forests (White 1994b).

Logging had the following effects on forest structure and function (Chapman & Chapman 1997):

1. Growth rates in the most heavily logged areas were consistently lower than in the unlogged areas.
2. The lightly logged areas had similar growth rates to unlogged areas in the small size classes. Trees in the 300 to 500 mm dbh size cohort though showed elevated growth rates relative to the unlogged areas.
3. Mortality was highest in the heavily logged areas. Many deaths were occurring when healthy trees were knocked over by neighbouring tree falls (incidental damage).
4. There was no difference in the density or species richness of seedlings in the logged and unlogged areas.
5. Sapling density was lower in the heavily logged areas, thus suggesting a high level of seedling mortality in logged areas.

Chapman & Chapman (1997) suggest that the opening of the canopy cover which is created during logging, the lack of aggressive colonizing tree species, the activity of elephants that is concentrated in logged areas, and an aggressive herb community (also: Wrangham *et al.* 1993b), all combine to delay vegetation recovery after logging in Kibale Forest.

Lwanga *et al.* (2000) investigated the tree dynamics in Ngogo, Kibale Forest, Uganda, from 1975 to 1998. In that period species richness decreased by 3%, species diversity (H') declined slightly from 2.97 to 2.86, the number of trees recorded in the sample plots (height ≥ 10 m) decreased by 8%, and the basal area decreased from 49.48 m²/ha to 48.68 m²/ha (Lwanga *et al.* 2000). Only for a small number of tree species did stem abundance and basal area increase (Lwanga *et al.* 2000). Since the overall decrease in density at Ngogo was not accompanied by a significant decrease in basal area the authors conclude that the majority of trees that had died were small trees and that this loss of basal area was compensated for by the growth of larger trees (Lwanga 2000). Furthermore, the distribution of size classes for evaluated trees also showed that the smallest size class exhibited the largest decline in density (Lwanga *et al.* 2000).

A comparative study at Kanyawara, Kibale Forest, Uganda, showed that the same tree species which declined or did not change in number in Ngogo increased in number in Kanyawara (Lwanga *et al.* 2000). The authors suggest that more favourable light conditions on the forest floor in Kanyawara might favour seedling survival and sapling recruitment at that site (Lwanga *et al.* 2000).

Different tree species start fruit production at different ages. When considering a logging operation for timber extraction in a forest inhabited by (frugivorous) primate species, this fact should be taken into account. If a sufficient number of trees and tree species, which start fruit production at an early age, are kept and given the chance to recolonize in sufficient numbers, selective logging in a primate rain forest habitat should be possible without causing ever-lasting damage and/or decline of the primate species (Lwanga *et al.* 2002).

CHIMPANZEE SOCIAL STRUCTURE AND BEHAVIOUR

"The classic problems of survival in the wild are finding food, escaping predators and parasites, and avoiding bad weather. For chimpanzees, the set of solutions adopted by even a single population is surprisingly diverse..." (Wrangham 1994).

Community structure

Chimpanzees live in *fission-fusion* societies which are defined as follows: "social groups in which all members are rarely, if ever, together as a spatially discrete unit, and in which stable subgroups of specific adults do not recur daily, as one-male harems do." (Ghiglieri 1984).

This rare form of social system between mammals consists of a number of subgroups forming a community, which constantly varies in size and composition of their members over time (Kortlandt 1962, Reynolds 1967, Baldwin *et al.* 1982, Ghiglieri 1984, Cox *et al.* 2000). A *community* is defined here as "a group of chimpanzees acquainted with and tolerating one another" (Baldwin *et al.* 1982). Gagneux *et al.* (2001) give the typical community size as between 20 to 100 individuals.

Different authors have observed and described different numbers and kinds of groups. Kortlandt (1962) distinguished two different group forms in Zaïre, namely (1) *sexual groups* mainly formed by adult males and childless females, but often including a few mothers and infants, and (2) *nursery groups* consisting mainly of juveniles up to the age of puberty, the mothers of these juveniles and sometimes one or two of the adult males. Reynolds & Reynolds (1965a) distinguished four different group forms in Uganda's Budongo forest chimpanzees, i.e. (1) *bi-sexual adult parties*, (2) *all-male parties*, (3) *mother parties*, sometimes with childless females, and (4) *mixed parties*, i.e. a combination of all-male and mother parties. Suzuki (1969) coins the term *nomadic group* and defines it as a group "whose stability, in terms of time, is unknown but which has a certain behavioural coherence in its nomadic life in natural surroundings". The

author then distinguishes five different types of nomadic groups in the savanna woodland of the Kasakati Basin at the eastern shore of Lake Tanganyika, western Tanzania, namely (1) *mixed nomadic groups*, (2) *adult nomadic groups*, (3) *mother nomadic groups*, (4) *male nomadic groups*, and (5) *lone individuals* (Suzuki 1969). Suzuki (1969) concludes that in general this area shows two forms of nomadic groups of chimpanzees, i.e. (1) lone individuals and (2) mixed nomadic groups containing individuals of both sexes and of various ages centring around one or more adult males.

On the other hand Goodall (1986) distinguishes eight different types of groups for the chimpanzees at Gombe, Tanzania, namely (1) *all male parties* of adult and/or adolescent males, (2) *a family unit* consisting of a mother and dependent offspring, at occasions including older offspring, (3) *nursery-units*, groups of family units that may include unrelated, childless females, (4) *mixed parties* of adult and/or adolescent males and females, (5) *sexual parties*, a mixed party with one or more females in oestrus, (6) *consortship* - exclusive relationships between an adult male and an adult female, (7) *gathering* - a large group containing at least one half of the community and one half of the adult males, and (8) *lone individuals* - single chimpanzees (Cox *et al.* 2000).

According to Ghiglieri (1984) chimpanzees aggregate in unstable travel and feeding parties and show a tendency to travel in "parties with non-random age-sex distribution" (Ghiglieri 1984). This author categorized chimpanzee travelling groups according to prevalent age-sex class representation and found that (1) *infants* always range together with their mothers, (2) *juveniles* often travel with their mothers and siblings, but they were also seen travelling solitary, with their siblings only or with parties containing no mothers and possibly also no siblings, (3) *sub adult males* mainly range with adult males though being reproductively inferior to them, (4) *adult males* range primarily with each other, (5) *adult females* travel mainly in units that consist of mothers and their dependent offspring, or in parties with other adult females, and (6) *adults of both sexes* sometimes travel with individuals of all life stages (Ghiglieri 1984).

Group sizes and composition change depending on habitat and season, and therefore reports differ from different research locations (Ghiglieri 1984). To be able to compare between-site group or party size Nishida (1994) suggests to firstly establish within-site party size reflecting daily, seasonal and annual change. As the most objective definition for *party size* he proposes "the largest party that includes at least one adult male (preferably the alpha male) in a day" (Nishida 1994). Chapman *et al.* (1994) list mean party sizes for chimpanzees and bonobos at different study sites summarized from different literature sources (Table 4.2).

Table 4.2: *Mean party sizes of chimpanzees at various locations in Africa (following Chapman et al. 1994)*

Study	Location	Mean party size
Ghiglieri 1984	Kibale (Ngogo), Uganda	2.6
Reynolds & Reynolds 1965b	Budongo, Uganda	3.9
Baldwin <i>et al.</i> 1982	Mt. Assirik, Senegal	4.0
Goodall 1968, 1986	Gombe, Tanzania	4.0
Chapman <i>et al.</i> 1994	Kibale (Kanyawara), Uganda	5.1
Sugiyama 1989	Bossou, Guinea	6.0
Nishida 1994	Mahale, Tanzania	6.2
Sabater Pi 1979	Okorobiko Mts., Equatorial Guinea	9.9
Teleki 1989	Tai, Ivory Coast	10.1

The ratio between adult females and males is > 1 in most chimpanzee communities (Ghiglieri 1984, Cox *et al.* 2000). Ghiglieri (1984) attributes this fact mainly to three different factors, namely (1) that females reach maturity a year or two earlier than males, (2) that females often temporarily emigrate to a neighbouring community, and might be included in both community counts, and (3) that it is mainly males who engage in displays and intercommunity combats and who might therefore be more frequently subject to accidental death or killing.

Ghiglieri (1984) gives the following age-class definitions for chimpanzees:

Infant:	0 - < 5 years
Juvenile:	5 - < 10 years
Sub adult:	10 - < 15 years
Adult:	≥ 15 years

Sugiyama (1969) in Ghiglieri (1984) additionally recognises babies (< 0.5 years) and classifies infants from 0.5 to 2 years only. Reynolds (1967) gives the age of sexual maturity for female chimpanzees between 7 and 10.75 years, and for male chimpanzees from 7 to 8 years. According to Goodall (1986) a chimpanzee is only considered to be an adult after s/he has reached sexual and social maturity.

Adult females frequently leave their home community and migrate to neighbouring communities to mate with the adult males there, so called "female exogamy", thereby ensuring a continuous mixing of gene pools (Ghiglieri 1984, Cox *et al.* 2000). Female chimpanzees give birth to an infant about every three to five years (Reynolds 1967, Goodall 1998) with pregnancy lasting an average of eight months (Kingdon 1997). According to Wrangham *et al.* (1994b) and Sugiyama (1989) mean interbirth interval ranges from 4.4 to 6.0 years, whereas Teleki (1989) estimates the average birth interval at 5.6 years and the beginning of a female chimpanzee's reproductive period at 12 years of age. Infants are normally nursed up to four or five years of age, while constantly being carried around by their mothers until at least three to four years of age. Yet, full independence only occurs around eight years of age (Goodall 1986, Teleki 1989). Infants who are orphaned before five years of age normally have a very small chance of survival even under normal wilderness conditions (Goodall 1986, Teleki 1989). Considering an expected reproductive span of about 25 years on average, the total number of offspring per female chimpanzee is not more than five per lifetime (Teleki 1989).

The existence of a male social network and a separate female social network has been established. The latter is considered to be much looser than the former, in most chimpanzee communities. The closer social interaction of male networks manifests itself for example in the fact that males groom each other much longer and more frequently than females interact in this way (Ghiglieri 1984, Nishida 1994, Cox *et al.* 2000). Furthermore, the range covered by the two networks is often not identical. The female network is considered to cover a smaller area of the community's home range but extends into the home range of a neighbouring community. The male network frequently covers the whole community home range, e.g. on patrol rounds (Ghiglieri 1984, Wrangham *et al.* 1994b, Cox *et al.* 2000).

When two different communities encounter this can result in extreme aggression, during which some members of the communities might even be killed and/or one of the communities might be dissolved as a result of this encounter (Goodall 1986, 1998, Cox *et al.* 2000).

Cognitive abilities

In a number of feeding experiments with six young, captive chimpanzees Menzel (1971, 1972) made some interesting discoveries concerning chimpanzees' spatial memory and their conversation about the environment.

The author discovered that in food hiding experiments chimpanzees will follow the one animal in the group who was present when the food items were hidden. This animal (a number of different individuals throughout the whole experiment) was able to remember the hiding place in the majority of cases (Menzel 1971). The leader of the group is also able to communicate to her/his ignorant companions whether the hidden item is a very desirable or less desirable food item or even a supposedly dangerous animal (e.g. a rubber snake) as well as information about the quantity of items hidden at one place (Menzel 1971).

Even if several food items were hidden at several locations the tested individual in most experiments remembered the majority of localities. When retrieving the items s/he followed the 'least distance principle' even in 'delayed response' tests (Menzel 1972). If several items were hidden non-randomly the chimpanzees would first recover the items in the area where most food samples were located and only then concentrate on the area with lower sample density (Menzel 1972). They would also first recover the preferred food items before recovering the less preferred items, while still following the least distance principle within each of the two categories, so-called 'cognitive mapping' (Menzel 1972).

This demonstrates immense cognitive and communicative abilities, but Menzel (1971, 1972) was not able to discover how the acquired and partly also processed information was passed on from the test animal to the ignorant control individuals in the group.

Locomotion

Chimpanzees are basically terrestrial but also arboreal, and they are able to travel four-, three- and two-legged (Kortlandt 1962, Reynolds & Reynolds 1965a, Reynolds 1967).

Doran & Hunt (1994) compared the locomotor behaviour of two chimpanzee subspecies (*Pan troglodytes schweinfurthii* from Mahale and Gombe, Tanzania, and *Pan troglodytes troglodytes* from Tai Forest, Ivory Coast) with each other and with the locomotor ability of the bonobo (*Pan paniscus* from Lomako, DRC). They distinguished five different categories of postural activity: (1) quadrupedalism, (2) quadrumanous climbing and scrambling, (3) suspensory behaviour, (4) bipedalism, and (5) leaping and diving. The authors concluded that there is far less variation in locomotor behaviour between sites and between subspecies than there is between the two species. Furthermore, they discovered that bonobos are more suspensory than chimpanzees and engage in more arboreal travel than chimpanzees who use terrestrial travel to move from one feeding place to the next (Doran & Hunt 1994).

Culture

Imanishi (1952) as cited in Wrangham *et al.* (1994b) defines *culture* as “socially transmitted adjustable behaviour”.

The existence of culture in chimpanzee populations manifests itself for example in the existence of different tool using techniques by different chimpanzee communities in different countries and locations (Wrangham *et al.* 1994b, Cox *et al.* 2000). For example, while chimpanzees in Tongo, DRC, use moss sponges to soak up water from tree holes, the chimpanzees in Gombe, Tanzania, use leaf sponges, but the chimpanzees in Kibale Forest, Uganda, prefer the use of stem sponges for the same purpose (Goodall 1986, Wrangham *et al.* 1994b). On the other hand even though, ecological conditions and food availability may be quite similar for different chimpanzee communities at different locations, their food use may still vary considerably (Wrangham *et al.* 1994b, Cox *et al.* 2000).

The possession of *culture* is a special asset of chimpanzees and the great apes in general, which makes it even more difficult to draw a clear line between human and non-human primate societies.

Predators

Besides leopard and lion the main predator of chimpanzees is man (Kortlandt 1962, Reynolds 1967, Ghiglieri 1984, Nishida 1994). Ghiglieri (1984) also assumes spotted hyena to be a potential predator as well as crowned hawk-eagles who might also be a danger for infant chimpanzees. Captive chimpanzees when faced with stuffed leopards use sticks or throw stones to fend the potential predator off (Kortlandt 1962, Reynolds 1967).

Man, apart from hunting chimpanzees for bush meat, also constitutes a deadly threat through his use of snares and other devices to catch forest-dwelling small ruminants, like duikers. Especially young, inexperienced chimpanzees get caught in these snares and often only escape at the price of the loss of a hand or foot if not their life through gangrenous infection (Ghiglieri 1984, Ammann 1997-1998).

A rare and unexpected predator for the chimpanzee is the chimpanzee-self: Goodall (1998) reports on several infanticides followed by cannibalism by one of the adult females and her daughter among the Gombe chimpanzees.

Destructive behaviour

During their displays and also when leisurely sitting on tree branches while eating fruits and leaves or when building nests chimpanzees cause a lot of serious damage to the vegetation which constitutes part of their natural diet and shelter (Reynolds 1967, Baldwin *et al.* 1982, Ghiglieri 1984, Wrangham *et al.* 1994b, Grieser Johns 1996, Goodall 1998, Voysey *et al.* 1999a).

Reynolds (1967) lists several such activities in the Budongo Forest, Uganda: drumming on tree buttresses, drumming (rapid locomotion), throwing and shaking things (Reynolds 1967).

Baldwin *et al.* (1982) consider chimpanzee nests to be "reliable and durable traces of the distribution of chimpanzees", which indicates the permanent state of destruction of branches and leaves used for the construction of night and to a lesser extent also day nests. As an indicator for

the life span of chimpanzee nests Ghiglieri (1984) used the “gradual recuperation of the tree”.

When evaluating responses of chimpanzees to habituation and tourism in the Kibale Forest of Uganda Grieser Johns (1996) used the presence of *feeding noises* as one possible strategy to indicate and locate the presence of chimpanzees. She defines *feeding noises* as “... the tearing of branches, stripping of leaves off branches, munching noises” (Grieser Johns 1996).

Goodall (1998) gives a number of examples of Gombe chimpanzees accidentally or wilfully destroying vegetation during their everyday activities, such as displaying, infants playing, feeding and nesting. All these activities are potentially destructive to the trees and other vegetation used by the chimpanzees.

Voysey *et al.* (1999a) comment on the price trees have to pay if relying on great apes as seed dispersers. They believe that the tree’s architecture, the structural quality of its wood and the position of fruits play an important role in the degree of damage a tree suffers for the benefit of seed dispersal by great apes (Voysey *et al.* 1999a) The authors also observe that trees specialised on great apes as seed dispersers seem to suffer less damage than generalists (Voysey *et al.* 1999a). Wrangham *et al.* (1994a) describe the destructive method of fruit collection by chimpanzees as follows: “ripe fruits were collected from small limbs that had been broken off by chimpanzees during their feeding”. Van Hooff (1973) gives two examples of tree destruction by captive chimpanzees: (1) he observed apes at Holloman Air Force Base in New Mexico to tear off leaves, branches and bark from trees provided in the enclosure, and (2) found apes at Arnhem Zoo to peel off the bark from trees in their enclosure since they favoured the taste of the former’s soft inside. Van Hooff (1973) expects those trees to eventually face complete defoliation and to “become one huge climbing frame in which the animals will be fully visible to the public” (Van Hooff 1973). Wilson & Elicker (1976) describe the waving of branches as one major component of displays performed by chimpanzees they released on Bear Island, Georgia, U.S.A. A similar destructive influence might be expected by chimpanzees when foraging for fruit in trees. Kortlandt (1960/61) ascribes the presence of a number of dead tree stumps inside a chimpanzee enclosure at the Institut Pasteur at Kindia in former French Guinea to the fact that all sprouts were generally eaten by these great apes. The author concludes that the destructive behaviour of chimpanzees through displays and sprout eating will lead over time to the complete destruction of woody vegetation in confined enclosures, such as zoos (Kortlandt 1960/61).

Jenkins (pers. comm.⁴) describes his experience when holding a group of originally 12 later 14 chimpanzees in an enclosure of 2.0 to 2.5 ha at Boki Ogi, Nigeria. The fenced-off area was completely covered with secondary rain forest. The chimpanzees ranged from 2.5 to 9 years and had a female:male ratio of approximately 1:1 (Jenkins pers. comm.). Chimpanzees were fed supplementary and water was freely available (Jenkins pers. comm.). The chimpanzees took about three to four years to completely destroy the secondary rain forest vegetation cover inside their enclosure (Jenkins pers. comm.). The destruction of trees was caused in the lower layers by playing infants, in the middle layers by fruit eating chimpanzees and in the high tree layers by the nest-building activities of adult chimpanzees (Jenkins pers. comm.).

Oppenheimer & Lang (1969) found that *Gustavia* trees had significantly more branches at a site *with* cebus monkeys than in a similar control site *without* monkeys. They suggest that the removal of terminal buds by the monkeys during feeding might release the lateral buds from apical dominance and thus induce increased branching (Oppenheimer & Lang 1969). An effect that might also be caused by chimpanzees feeding on buds in different fruiting trees.

Figures 4.8 to 4.17 show the destruction caused by chimpanzees (1) at Ngamba Island Chimpanzee Sanctuary (Figures 4.8 – 4.12) and (2) at Sweetwaters Chimpanzee Sanctuary in Nanyuki, Kenya (Figures 4.13 – 4.17).

⁴ Jenkins, P. 2001. Pandrillus, Calabar, Nigeria.



Figure 4.8: Young tree on Ngamba Island that has been defoliated and its branches broken off by infant chimpanzees during their forest walks.



Figure 4.9: One branch of a young tree has been broken off (arrow) by adult male chimpanzees displaying while foraging through the secondary rain forest on Ngamba Island.



Figure 4.10: Destruction caused to the undergrowth by adult chimpanzees while foraging, playing and feeding in the secondary rain forest on Ngamba Island.



Figure 4.11: Branches and stems of woody vegetation are bent and broken by the chimpanzees during their daily visits to the secondary rain forest on Ngamba Island.



Figure 4.12: An adult chimpanzee at his 'destructive work' in a tree on Ngamba Island.



Figure 4.13: Trees defoliated by chimpanzees at Sweetwaters Chimpanzee Sanctuary, Nanyuki, Kenya – with kind permission from A. Olivecrona, Sanctuary Manager.



Figure 4.14: Destruction of woody vegetation caused by chimpanzees at Sweetwater Chimpanzee Sanctuary, Nanyuki, Kenya – with kind permission from A. Olivecrona, Sanctuary Manager.



Figure 4.15: Destruction of woody vegetation (close up) at Sweetwaters Chimpanzee Sanctuary, Nanyuki, Kenya – with kind permission from A. Olivecrona, Sanctuary Manager.



Figure 4.16: Adult chimpanzee hunching next to a destroyed young tree at Sweetwaters Chimpanzee Sanctuary, Nanyuki, Kenya – with kind permission from A. Olivecrona, Sanctuary Manager.



Figure 4.17: Adult chimpanzee in 'display mood' with his hair slightly bristled – the tree in the background shows destruction caused by chimpanzees at Sweetwaters Chimpanzee Sanctuary, Nanyuki, Kenya – with kind permission from A. Olivecrona, Sanctuary Manager.

Chimpanzee ranging patterns

Animals living in groups share an area of land within which they forage, sleep, raise their young, and go about their other daily activities. The area so occupied is called 'home range' (Goodall 1986) and its size depends on a number of factors. The more important of those being: (1) the size and food requirements of the animal, (2) the number of individuals in the group, (3) the density of surrounding populations, and (4) the type of habitat (Goodall 1986).

According to Kortlandt (1984) the need for a very varied diet is the underlying factor determining the size of the home range of the chimpanzee. This need furthermore determines the carnivorous habits and the social organisation of this great ape species (Kortlandt 1984). Baldwin *et al.* (1982) give as general definition for chimpanzees' home range "the total area used for at least one year by members of a community of chimpanzees".

Metabolic principles

McNab (1963) examined the relationship between the size of the home range and mammalian body size. According to the author the size of the home range in wild mammals is determined by the rate of metabolism which in turn is dependent on body mass.

Following Kleiber's (1961) equation in McNab (1963) the basal rate of metabolism is calculated as follows:

$$M = k W^{0.75} = 70 W^{0.75}$$

where: M = basal metabolic rate [kcal/day]

W = body mass [kg]

k = constant equal to 70.

Since there is also a linear relationship between the \log_{10} of home range plotted against the \log_{10} of body mass, in that the cost of locomotion per unit body mass is lower for larger animals which are thus expected to have larger home ranges (Schmidt-Nielsen 1972), the size of home range can eventually be expressed as being determined by the basal rate of metabolism:

$$R = 0.12 M$$

where: R = size of home range [acres].

This equation represents just an approximation of the real relationship since it uses basal metabolic rate instead of total daily energy expenditure which would furthermore be temperature dependent (McNab 1963).

McNab (1963) found that the size of a species' range was dependent on the type of food this species consumes. He thus divided mammals into two broad categories, *food hunters* and *food croppers*. While the former have to 'hunt' for their food and include those species that are either granivorous, frugivorous, insectivorous, or carnivorous, the latter usually do not need to 'hunt', therefore have a smaller home range, and include those species that are either grazers or browsers (McNab 1963).

McNab (1963) adjusted his equation to correct for this difference in home range size for the two separate types of mammals, resulting in:

$$R_h = 0.20 M \text{ (for hunters)}$$

$$R_c = 0.05 M \text{ (for croppers).}$$

Thus, *food hunters*, like the chimpanzee, have about four times the home range size of *food croppers* with the same body mass.

This equation still does not consider the direct and indirect influences of weather and climate on the animal. Furthermore, it does not account for the fact that species with large home ranges usually cannot maintain locally dense populations because of the limited amount of energy available within a given area (McNab 1963).

Milton & May (1976) have developed McNab's equation further. These authors divide primates into (1) folivores, i.e. species who depend on mature or immature foliage as their staple diet, (2) frugivores, i.e. species who are primarily fruit eaters and take only a small amount of foliage and little or no protein, (3) generalist primary consumers, i.e. species who eat roughly equal proportions of both foliage and fruit and little or no animal protein, and (4) omnivores, i.e. species who seem to actively seek out and probably depend on animal protein (Milton & May 1976). The authors attribute frugivorous and omnivorous primates to McNab's *hunters* in their feeding habits and folivorous primates to McNab's *croppers* (Milton & May 1976). Milton & May (1976) conclude that folivorous primates occupy a smaller home range area for their body mass than do frugivorous and omnivorous primates. The authors furthermore state that primates in general

occupy a smaller home range area per individual than solitary terrestrial mammals do, while primates living in social groups have a much larger total home range than individual solitary mammals (Milton & May 1976). Milton & May (1976) give three main factors which determine home range size, i.e. (1) *body size* of the animal, (2) *–vory* of an animal, e.g. frugivores tend to have larger home range sizes than folivores, and (3) *height of the tree canopy*, since the size of this third dimension adds to the density of resources per area and to the actual distance travelled in space per unit area and has an especially marked effect on the size of the home range of folivorous primates. Taking these considerations into account the authors arrive at the following equation to calculate the size of home range of individual *primate hunters*, which includes the chimpanzee (Milton & May 1976):

$$\text{Log } HR_i = 0.83 \text{ Log } BW - 2.17$$

With HR_i = size of home range [ha] of the individual
 BW = body mass [g].

Milton & May (1976) are aware of certain shortcomings of this equation but consider it valid to at least give some idea of the relative amount of space required to provide adequate resources for individuals of a species.

Ghiglieri (1984) uses the same equation to calculate the home range for a single chimpanzee at Ngogo, Kibale Forest, western Uganda. He estimates the mean mass of an individual as 28.7 kg and arrives at a home range portion per Ngogo chimpanzee of 34 ha or 0.34 km². This would lead to a community home range for the 55 chimpanzees in his study group of 18.6 km², while from his census and nest count data the author estimated a home range of between 23.1 to 37.9 km² for the Ngogo community (Ghiglieri 1984). Ghiglieri (1984) criticises the equation developed by Milton & May (1976) in that it inherently underestimates the home range of chimpanzees. The reasons for that being that firstly the habitat type is not taken into account and secondly the diet has been generalized to that of a hypothetical model omnivore rather than that of a frugivore who has more specific and demanding foraging requirements (Ghiglieri 1984).

Home range and habitat type

Kortlandt (1984) criticises all above equations since they do not take into account the immense need for diversity of the chimpanzee's diet. According to him the minimum food diversity required for nutritional reasons mainly determines the necessary home range area for an individual and a

community of chimpanzees in a given habitat (Kortlandt 1984). Based on this statement is the conclusion that in a habitat with a low or normal botanic diversity but a high carrying capacity, the number of chimpanzees in a community would amount to:

Population = range with minimum diversity x carrying capacity

With the size of the community being determined by the minimally required locomotor performance and the carrying capacity of the habitat (Kortlandt 1984).

In a habitat with a high botanical diversity but a quite low carrying capacity the number of chimpanzees in a community would amount to:

Population = maximum range x carrying capacity

With the size of the community being determined by the maximum (efficient) locomotor performance and the carrying capacity of the habitat (Kortlandt 1984).

The term *carrying capacity* has largely been replaced by the term *ecological capacity of the area*. Kortlandt (1984) uses the term *carrying capacity* to describe the long-term equilibrium of a population of animals under specific habitat conditions (Bothma 1996).

Contrary to what is normally found among the other great apes and many monkeys, in none of the two above cases is the community size determined by ethological mechanisms and social interaction processes. It appears that the higher sociality of the chimpanzee, as compared with other great apes and monkeys, is an adaptation to his need for a wide diversity of foods (Kortlandt 1984). Following Kortlandt (1984) this finding would also explain the fact that rain forest-dwelling chimpanzees form larger communities than their woodland-, savanna- and mosaic-dwelling conspecifics. This is again contrary to the general rule when comparing (smaller) forest-dwelling with (larger) open-land dwelling mammalian communities (Kortlandt 1984).

Female and male home range patterns

Goodall (1986) states that chimpanzees who live in a relatively lush environment, such as Gombe, have smaller home ranges than chimpanzees inhabiting harsher and more arid parts of Africa. She also mentions that differences exist in home range sizes of individual chimpanzees depending on their age, sex and reproductive status and depending on the year.

The author recorded a distance of 3.0 – 5.0 km travelled per day for an alpha male. A pregnant female travelled a lowest mean of 2.4 km per day in the third week of August 1977, while a

female in oestrus travelled a mean of 3.1 km per day. A male and female pair only travelled a mean of 1 km per day during their consortship (Goodall 1986).

Kordtlandt (1984) gives the following examples of community sizes and foraging habitats in mosaic and savannah-woodlands as compared to rain forest habitats:

Table 4.3: Community sizes and foraging ranges of chimpanzees (following Kortlandt 1984, using his corrections of range sizes)

Community	Population	Range [km ²]
<i>Mosaic and savannah-woodland habitats</i>		
Gombe, Gombe River	20 - 30	13.0 – 21.0
Mahale Mountains, K-Group	26 - 34	10.5
Kasakati, Group L	40	122.0
<i>Rain forest habitats</i>		
Budongo, Eastern Valley	56	7.5
Bukavu-Walikale	65 - 91	50.0
Pygmy Chimpanzee	45 - 50	22.0

Goodall (1986) defines the *year range* of an individual chimpanzee as “the sum of all areas visited during a given year”. As might be expected, her observations showed that the year range of a healthy adult male is larger than that of a healthy anoestrus adult female. For the years 1972/73 she gives the year ranges for adult males between 9 to 12 km², with a median of 10.3 km²; while for three anoestrus females in the same period of time the year ranges where from 5.8 to 7.0 km² travelled, with a median of 6.8 km² (Goodall 1986).

Goodall (1986) defines the *community range* according to Wrangham (1977) as “the sum of all areas visited by each adult male of the community during a given year”. The authors found that the community range of the chimpanzees at Gombe changes over time primarily as a result of changes in the number of adult males in the community from year to year (Goodall 1986).

Goodall (1986) furthermore distinguishes *core areas* and *boundary areas* of a community's home range. While male chimpanzees tend to visit each of the home range's boundary areas about every four days, female chimpanzees, at least when in anoestrus, spend the majority of their time in the core area of the community's home range (Goodall 1986). Additionally, chimpanzees shift their ranges in response to the seasonal fruiting patterns of desired or required species of food (Baldwin *et al.* 1982).

Chimpanzee densities

Teleki (1989) gives general guidelines regarding chimpanzee densities in different habitat types. The author defines *crude density* as a derivative of *population size* and *habitat size* and from his literature study arrives at the conclusion that crude densities of chimpanzees at the most intensely studied sites range from as low as 0.1 to as high as 6.8 chimpanzees per km², with an average density far below 1.0 chimpanzee per km² (Teleki 1989). As a general rule Teleki (1989) states that in the marginal dry savanna-woodland habitats (e.g. Mt Assirik, Senegal), the average density is about 0.1 chimpanzees per km², while for moist mosaic habitats of grassland-woodland forests (e.g. Gombe, western Tanzania) this density is about 0.2 chimpanzees per km², and for the rain forest habitat an average density of 0.3 chimpanzees per km² might be assumed. However, densities in this habitat show great variations from higher densities of about 4.0 to 6.8 chimpanzees per km² (Budongo Forest, Uganda) to lower densities from 0.4 to 2.0 chimpanzees per km² (Bwindi and Kibale Forest, Uganda, respectively) (Teleki 1989). Especially, since poaching has become a serious problem the author considers the former high density estimates to be particularly anomalous and therefore decides to adjust the mean density for a rain forest habitat even below the lower estimated values (Teleki 1989). Teleki (1989) thus

considers the baselines figures of 0.1, 0.2, and 0.3 chimpanzees per km² to be the best options for projecting wild chimpanzee population numbers across tropical Africa. Table 4.4 lists examples of chimpanzee densities in different habitat types taken from different literature sources.

Table 4.4: *Chimpanzee densities in different habitat types (habitat types according to Teleki 1989)*

Source	Location	Habitat	Density [chimpanzees/km ²]	Range [km ²]
Baldwin <i>et al.</i> 1982	Mt Assirik Senegal	Dry savanna-woodland	0.09	239
Tutin & Fernandez 1991	Lopé Reserve Gabon	Primary rain forest	1,00	unknown
Bermejo 1999	Odzala NP* Republic of Congo	Primary & Marantaceae forest	2.20	2 848
Hart & Hall 1996	Maiko NP DRC	Primary rain forest	0.46	10 830
Hart & Hall 1996	Kahuzi-Biega NP DRC	Primary rain forest	0.40	6000
Hart & Hall 1996	Okapi WR** DRC	Primary rain forest	0.89	13 700
Albrecht 1976	Budongo Forest Uganda	Primary rain forest	1.45 – 1.95	Unknown
Ghiglieri 1984	Kibale Forest Uganda	Primary rain forest	1.45 – 2.38	~70
Goodall 1998	Gombe NP Tanzania	Grassland-woodland forest	~2.10	~78

* NP = National Park ** WR = Wildlife Reserve

Chimpanzee nest-building behaviour

According to Fruth & Hohmann (1994) chimpanzees spend at least 50% of their lives on nests. The authors assume therefore that these great apes can be expected to choose their nesting sites carefully (Fruth & Hohmann 1994).

Despite variation related to individual, age or species, all nests constructed by the great apes share three major components constructed by combining plant material: (1) a solid foundation, (2) a central mattress, and (3) a lining made of additional leaves and twigs (Fruth & Hohmann 1994). The technique of nest making entails bending down branches of the surrounding bushes. Though this is not done in a particular order it is still ensured that they criss-cross one another and eventually form a platform on which the ape can sit or stand. Thereafter, all the tops of the branches are bent into a ring resting on the platform (Bolwig 1959).

There are day nests and night nests, the former being much more casually constructed and also used for a much shorter period of time than the latter (Baldwin *et al.* 1981, Fruth & Hohmann 1994, Goodall 1998).

Baldwin *et al.* (1981) compare nests made by different populations of chimpanzees in different habitats – *Pan troglodytes troglodytes* in a forested area in Equatorial Guinea and *Pan troglodytes verus* in a savanna habitat in south eastern Senegal. The authors concluded that all the differences they found in nest-building between populations could be explained by environmental factors (Baldwin *et al.* 1981). It was found that at Mt Assirik, Senegal, the height of nests was highest in the gallery forest, then in grassland and lowest in woodland. The tallest trees occur in the gallery forest, but trees in the grassland are considered lower than in the woodland. When examining the trees chosen for nesting in grassland, it became obvious that the chimpanzees preferred those species which grow along seasonal watercourses, e.g. *Spondas mombin* and *Adansonia digitata*. These species occur only rarely in a grassland habitat, but when they do so, they are exceptionally tall for this type of habitat (Baldwin *et al.* 1981). The average heights for nests were 12.2 m at Ngogo and 10.8 m at Kanyawara, 16.5 m near Fort Portal and in the Ruwenzori (Bolwig 1959, Ghiglieri 1984). Ghiglieri (1984) attributes these differences mainly to “differences in vegetative physiognomies between habitats”

Ghiglieri (1984) found that the chimpanzees in Kibale Forest prefer certain tree species for the construction of their day and night nests. The author concluded that factors influencing this pattern of utilization are “the tensile suitability of the tree’s limbs”, its “density of foliage” and its

proximity to a highly favoured food source (Ghiglieri 1984). Hashimoto (1995) found a similar preference for certain tree species used for nest building among chimpanzees in the Kalinzo Forest, Uganda.

According to Fruth & Hohmann (1994) chimpanzee infants already start at the early age of eight months with their first attempts at nest building. These first attempts are still a long way off from the sophisticated structures an adult chimpanzee will construct. Especially day nest construction increases in frequency and reaches a peak when the infant is about three years old. Therefore, long before weaning, nest building becomes an important part of the behaviour of infant chimpanzees (Fruth & Hohmann 1994).

Chimpanzee feeding behaviour

“The Gombe chimpanzees can be described in summary as omnivorous forager-predators that supplement a basically vegetarian diet in various ways, including the optional practice of hunting other animals, with fellow primates being their most favored prey” (Teleki 1973).

Diet composition

Clutton-Brock & Harvey (1977) divide primates in general into three dietetic groups: insectivores, folivores and frugivores with the chimpanzee being a member of the latter group. The authors found that interspecific differences in the dietetic diversity in primates are positively related to body mass, day range length and home range size. While the proportion of day time spent feeding is positively related to body mass, but negatively related to the proportion of foliage in the diet (Clutton-Brock & Harvey 1977).

Chimpanzees are primarily frugivorous and spend between 46% to 62 % of their time feeding, between 25% to 39% resting, and only between 8% to 20% travelling (Wrangham 1977, Ghiglieri 1984, Isabirye-Basuta 1989, Erwin 1992). The major component (45 – 75%) of their diet is fruits, but, leaves, piths, shoots, seeds, bark, flowers, wood, galls, resin, clay, insects, rodents, suids, bovids, and primates, birds eggs and birds, clay and soil are also consumed (Hladik 1977, Goodall 1986, Erwin 1992). According to Sugiyama & Koman (1987) fruits and seeds (nuts) occupy more than half of the chimpanzees’ diet; and leaves, shoots, and twigs (stems) constitute about another third. At Gombe chimpanzees have been observed to eat 184 items of vegetable food from 141 species of trees and plants (Goodall 1986). Also according to Hladik (1973) and Wrangham (1977) fruit and leaves constitute the major part of the chimpanzee’s diet. Fruits may

form up to 90 % of the daily diet and never less than 40%, with most of the daily fruit consumption being between 55% and 80% (Hladik 1977). At the same time there is a daily intake of animal food of between 2.5% to 6.0%, mainly consisting of ants, some termites, bird eggs and fledglings (Hladik 1977). Newton-Fisher (1999) found that recently habituated chimpanzees of the Sonso community in Budongo Forest, Uganda, spent an average of 64.5% of their time eating fruit and of 19.7% eating arboreal leaves.

A seasonal variation of the diet composition is noticeable and can be explained by the variation of the availability of food stuff over the year (Hladik 1973, 1974 & 1977, Sabater-Pi 1979, Goodall 1986, Tutin *et al.* 1991a, Wrangham *et al.* 1991, Newton-Fischer 1999). Table 4.5 lists the components of the chimpanzees' diet as determined in different study areas and habitats.

Table 4.5: Composition of chimpanzee diet in different habitats

Diet Component	Mean percentage of dietary composition [%]							
	1	2	3	4	5	6	7	8
Plant food	93	96	89	91.25	97.5	X	100.9	100
Fruit	(68)*	68	59	59.5	45	X	49.2	57
Leaves	(25)	(28)	17	25.5	32	X	(36.1)	(10)
Blossoms			4	4.75		X	6.3	10
Seeds	(68)		9	1.5	8	X	3.4	10
Shoot							(36.1)	(10)
Pith						X		
Bark	(25)				12.5	X	(5.9)	7
Stems	(25)	(28)					(36.1)	3
Wood						X	(5.9)	
Resin			X	X		X	(5.9)	
Root						X		3
Bananas (provisioned)	X**	X	X	X				
Animal food	6	4	7	5.75	2.5	X	X	X
Vertebrate prey		(4)	2	1		X	X	X
Mammals		(4)				X	X	X
Birds		(4)				X	X	
Eggs			X	X		X		
Reptiles								X
Fish	6						X	
Insects		(4)	4	4.5	2.5	X	X	X
Galls			1	0.25				
Soil	X	Trace						
Minerals	X					X		
Miscellaneous			4	3		X		

* all diet components in (brackets) contribute to the percentage given.

** an X is made if no percentage of total diet is given in the literature source.

Key:

1 = Hladik 1973, Ipassa, Gabon – *primary rain forest*.

2 = Hladik 1977, Ipassa, Gabon.

3 = Goodall 1986, Gombe, Tanzania, average for 1978 – *mosaic forest, woodland and grassland*.

4 = Goodall 1986, Gombe, Tanzania, average for 1979 – see difference in *seed* consumption to 1978.

5 = Sabater-Pi 1979, Okorobikó Mountains, Equatorial Guinea – *primary and secondary rain forest*.

6 = Nishida & Uehara 1983, Mahale Mountains, Tanzania – *mosaic forest, woodland and riverside*.

7 = Sugiyama & Koman 1987, Bossou, Guinea - *secondary rain forest of different stages*.

8 = McGrew *et al.* 1988, Mount Assirik, Senegal – *heterogeneous Sudanian savannah woodland*.

Factors affecting food choice

Food choice in the chimpanzee is primarily affected by variation in the levels of specific nutrients in different foods rather than by variation in secondary compounds. (Hladik 1977, McGrew 1985, Goodall 1986, Reynolds *et al.* 1998). Hladik (1978) supports the view that plant species are chosen for their nutritional quality. Regarding leaves young leaves are favoured, since they possess a greater amount of proteins and soluble sugars than mature leaves (Hladik 1978). The author concludes that it is therefore mainly the primary compounds of leaves that determine which plants are chosen for food; while the secondary compounds have less influence on vertebrate food choice (Hladik 1978). Hladik (1978) considers the impact of the vertebrate folivorous population on the leaf mass of the primary rain forest of Ipassa, Gabon, as being low, since these consumers do not eat more than one percent of the total leaf production. While the impact of insect folivory on leaf-production in this habitat may reach up to 10% of the total litter fall (Hladik 1978).

The occasionally observed feeding on termite clay by the chimpanzees of Gombe might have the effect of neutralizing tannins (Goodall 1986). However Tutin *et al.* (1991a) conclude that the small number of mature leaves eaten by the chimpanzee suggests a general avoidance of food with high fibre content and/or secondary compounds. Matsumoto-Oda & Hayashi (1999) found that *Pan troglodytes schweinfurthii* at Mahale Mountains, Tanzania, (1) eat fruit that contain significantly more non-fibrous carbohydrates than leaves, (2) of the six most important chimpanzee food items, four are fruits, (3) the important fruits contain significantly more non-fibrous carbohydrates than the unimportant fruits, and (4) fibre and condensed tannin content are negatively correlated with food selection.

According to Sabater-Pi (1979) the chimpanzee mainly chooses his food according to its typology, i.e. taste, smell, texture and abundance. However, Hladik (1977), Matsumoto-Oda & Hayashi (1999) and Wrangham *et al.* (1999a) all agree that chimpanzees choose their food items in such a way as to ensure a maximum yielding of nutrients and calories.

Overall, a diurnal rhythm in food choice can be observed, in that fruits tend to be eaten earlier in the day than leaves (Clutton-Brock 1977, Wrangham 1977, Sabater-Pi 1979, Ghiglieri 1984, Goodall 1986).

Isabirye-Basuta (1989) reports fruit utilization by chimpanzees at Kanyawara, in Kibale Forest, Uganda, was not related to fruit abundance. These apes select certain preferred fruit species

which they consume extensively even if their abundance is much lower compared to other fruit species available at the same time (Isabirye-Basuta 1989, Matsumoto-Oda & Hayashi 1999). Based on the number of plant species eaten each month, diet diversity was significantly inversely related to (1) fruit abundance, and (2) the proportion of fruit in the monthly diet (Isabirye-Basuta 1989). The number of plant species used (1) as fruit source, and (2) as food source, was significantly inversely related to the number of fruit species available (Isabirye-Basuta 1989).

According to Baldwin *et al.* (1982) and to Goodall (1986) the availability of water determines to a large extent the seasonal usage of different vegetation types by chimpanzees, especially in a rather arid savanna habitat.

White & Wrangham (1988) compared party size and feeding behaviour in chimpanzees and bonobos. They concluded that party size for both groups was dependent on the size of the food patch (also: Ghiglieri 1984, Isabirye-Basuta 1988); and that party size for feeding chimpanzees was larger in a forest habitat than in a mixed habitat with poorly developed forest (White & Wrangham 1988). Additionally, Isabirye-Basuta (1988) found that large-crowned trees support larger parties of feeding chimpanzees than small-crowned trees. Furthermore, the chimpanzees also feed and stay longer to socialize in the former than in the latter trees (Isabirye-Basuta 1988).

Chapman *et al.* (1994) compared the distribution of chimpanzees and bonobos in the fruiting trees composing a food patch. The authors observed that, while bonobos appeared to feed together in the same tree, the individual members of a chimpanzee party would disperse over several neighbouring trees, thus utilizing and affecting most of the trees in the food patch (Chapman *et al.* 1994).

Protein sources

Chimpanzees compensate for the low protein content of fruits by consuming young leaves with a higher protein content. They select insects for specific amino acids (Hladik 1977). Hladik (1977) gives the average protein content of the pulp of fruits as 5%, which is insufficient to compensate for the loss of nitrogen of an adult chimpanzee. Seeds which have an average protein content of 10.5 % cannot compensate for that. Leaves and stems have a high protein content (mean 24.9%) and are furthermore commonly available. Especially young leaves and shoots may thus be eaten when invertebrates or other animal prey cannot be obtained in sufficient quantity to complement the frugivorous diet (Hladik 1977). The essential amino acids for chimpanzees are

cystine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tyrosine and valine (Hladik & Viroben 1974). The chimpanzees of Ipassa consume stems (*Hypselodelphis* species), leaves (*Baphia* species), ant nests (*Macromisoides*), ants, eggs, larvae and pupae of *Ecophylla* and birds' eggs to replenish their need for essential amino acids (Hladik & Viroben 1974). The main source of protein for chimpanzees released on the island of Ipassa, near Makokou, Gabon, were ants (Hladik 1973).

Nishida & Uehara (1983) have observed the chimpanzees at Mahale Mountains, Tanzania, to feed on mammals, birds and insects as source of animal protein. Their mammal prey mainly consisted of primates and artiodactyles, e.g. *Galago crassicaudatus crassicaudatus*, *Colobus badius tephrosceles*, *Cercopithecus* spp., infant *Pan troglodytes schweinfurthii*, *Cephalophus monticola*, *Tragelaphus scriptus*, and *Potamochoerus porcus*. Other vertebrates come from the taxa Rodentia and Hyracoidea (Nishida & Uehara 1983). Bird prey species include *Francolinus squamatus* and *Gallus gallus*, the latter from neighbouring human settlements (Nishida & Uehara 1983).

Insects from the taxa Hymenoptera, Isoptera, Hemiptera, Coleoptera, Orthoptera, and Lepidoptera are observed prey species and eggs, larvae, pupae, workers, soldiers and reproductives are consumed in varying amounts from the different species (Nishida & Uehara 1983). Mammal prey is in most cases solely hunted and consumed by the male members of a chimpanzee community (Teleki 1973, Goodall 1986).

Sugiyama & Koman (1987) have observed the chimpanzees in Bossou, Equatorial Guinea, to use mammals, birds, fish, crustaceans, and insects as source of animal protein. While McGrew *et al.* (1988) list insects, reptiles and mammals as animal protein source for the chimpanzees at Mt Assirik, Senegal. These chimpanzees are the only population of wild chimpanzees known to concentrate on nocturnal prosimians (*Galago senegalensis* and *Perodicticus potto*) as prey (McGrew *et al.* 1988).

Matsumoto-Oda & Hayashi (1999) state that protein content is positively related with food selection in non-human primates. They examined fruits and leaves composing part of the diet of the Mahale Mountains chimpanzees in Tanzania. Their results showed that leaves contain significantly more protein than fruits, while the lipid content did not differ significantly for the two food items (Matsumoto-Oda & Hayashi 1999). The authors conclude that although fruits composing the natural diet of chimpanzees contain lower levels of protein essential for body building they still are an important resource of ready energy through their high content of non-

fibrous carbohydrates (Matsumoto-Oda & Hayashi 1999).

The importance of Ficus species

Wrangham *et al.* (1993a) investigated the differences in nutrient content of pulp and seeds of nine Ugandan *Ficus* species in Kibale Forest, Uganda. Figs are commonly eaten by Ugandan primates and also constitute a major component of the diet of chimpanzees in Kibale Forest (Wrangham *et al.* 1993a). Compared to the seed fraction of figs the authors found that the pulp fraction contains more water-soluble carbohydrates, complex carbohydrates, calories, and ash. The seed fraction, however, possesses more condensed tannins, lipids and fibre (Wrangham *et al.* 1993a). In their analysis the authors assumed that the seed fraction was totally indigestible, a fact that they admit to be an exaggeration (Wrangham *et al.* 1993a). Figs are an energy rich food with adequate protein (Wrangham *et al.* 1993a). The feeding rate of figs increased with increasing fig size, while at the same time, the harvesting rate of figs did not decline sharply with increasing fig size (Wrangham *et al.* 1993a). The feeding rate appears to have a more important effect on the rate of nutrient intake than the nutrient density of the fruit. Thus, even though larger figs have a higher water content than smaller figs, their consumption still leads to a higher nutrient intake per time interval. This higher intake resulted in an intake of more than 167.44 Joule per minute, excluding calories from insoluble fibre, when the chimpanzees harvested larger figs (Wrangham *et al.* 1993a).

A clear tendency was observed among the chimpanzees in Budongo Forest, Uganda, to feed on foods with high sugar content, while tannin content did not affect food choice (Reynolds *et al.* 1998). This latter finding contradicts the observation made by Tutin *et al.* (1991a).

When investigating two different *Ficus* species in Budongo Forest these authors found a significantly higher total sugar content (glucose, fructose, sucrose) and lower tannin content in the pulp compared to the seeds (Reynolds *et al.* 1998). *Ficus vallis-choudae*, has a three times higher tannin content than *F. sansibarica*, and is not eaten as often as *F. sansibarica* (Reynolds *et al.* 1998.)

Newton-Fisher (1999) observed the fig-eating behaviour of chimpanzees in Sonso, Budongo Forest, Uganda. He found that figs were eaten in most or all months of the year and thus considers them to be staple food for chimpanzees since they are so commonly consumed.

Terrestrial herbaceous food

Wrangham *et al.* (1991) distinguish four different plant food categories in the diet of chimpanzees in Kibale Forest, Uganda: (1) non-fig tree fruits, (2) fig tree fruits, (3) herbaceous piths, and (4) terrestrial leaves. The authors observed that chimpanzees eat piths primarily from herbaceous stems in the ground layer and they thus investigated the use of terrestrial fibrous or herbaceous food (THF) by unprovisioned chimpanzees (Wrangham *et al.* 1991). The authors conclude that pith, in time of food scarcity, is an important source of energy for these chimpanzees and thus classify THF as an important fallback food for the chimpanzee community in Kibale Forest (Wrangham *et al.* 1991).

In a second study Wrangham *et al.* (1993b) found a positive correlation between rainfall and pith intake by chimpanzees and baboons in Kibale Forest. They furthermore discovered that a thicker ground cover with THF appears in areas of the forest where (more) logging occurred. However, THF stem density is not positively correlated with the biomass density of edible food and can therefore not be used for predictions (Wrangham *et al.* 1991). The authors conclude that a thicker undergrowth, as the result of selective logging, does not necessarily mean an increase in THF and thus in high food density for apes (Wrangham *et al.* 1991).

Chapman *et al.* (1994) report that chimpanzees spend about 1.8% of their feeding time consuming THF. While doing so, their party sizes are smaller than when feeding in a fruiting-tree patch in the forest (Malenky *et al.* 1994).

Geophagy

According to Hladik (1977) geophagy is a common habit in chimpanzees. Chimpanzees in Gabon and at Gombe, Tanzania, were seen to ingest earth in pieces of about 10 to 20 g up to twice daily. Most of the earth ingested had been modulated by insects beforehand. Especially the cylindrical constructions ("chimneys") which are commonly built by Homoptera larvae of the species *Muansa clypealis* were frequently eaten by all members of the observed chimpanzee groups (Hladik 1977). The mineral content of the earth is generally lower than that of common chimpanzee food plants and does not seem to contribute significantly to the mineral nutrition of the chimpanzees. The most likely function of eating clay and other phyllosilicate material is to act as an absorbent for certain components of the stomach content such as tannins (Hladik 1977, Goodall 1986).

Mahaney *et al.* (1997) examined soil samples eaten by chimpanzees in Kibale Forest, Uganda. They found that the well weathered soils that were ingested had been formed in very fine-grained volcanic deposits (tuffs) and contained an abundance of metahalloysite. This substance is mineralogically and chemically similar to the pharmaceutical Kaopectate™ that alleviates diarrhoea (Mahaney *et al.* 1997). Mahaney *et al.* (1997) thus postulate that chimpanzees ingest soil in the Kibale Forest as a form of treatment for diarrhoea. The only other mineral prominent in these soil samples in any quantity to affect dietary or nutritional intake was iron (Mahaney *et al.* 1997).

Zoopharmacognosy

The observation that chimpanzees consume certain food stuff for therapeutic reasons has opened a new avenue of research called *zoopharmacognosy* (Nishida 1994).

Apart from the ingestion of metahalloysite (Mahaney *et al.* 1997) chimpanzees have been observed to ingest leaves of the genera *Vernonia* and *Aspilia* (Hladik 1977, Wrangham 1977, Wrangham & Nishida 1983, McGrew 1985, Nishida 1994). While a chemical analysis of *Vernonia* leaves showed compounds that are likely to be effective if ingested, an identical analysis for *Aspilia* leaves remained inconclusive (Nishida 1994).

Wrangham & Nishida (1983) describe how chimpanzees mainly consume these leaves early in the morning in contrast to most other foods that are eaten throughout the day. The chimpanzees do not chew these leaves, but one by one slowly suck young leaves in bouts of on average 15 min. The authors suggest that the active ingredient might be a stimulant. Since these leaves are consumed early in the morning they have a layer of moisture on their surface which might contain this ingredient in a soluble form as well as in a pharmacologically active concentration. Furthermore, *Aspilia* leaves are known to be used medicinally by indigenous African people (Wrangham 1977, Wrangham & Nishida 1983, McGrew 1985).

Provisioning

In a number of chimpanzee study sites the provisioning of food, i.e. bananas, has been used to facilitate habituation of wild chimpanzees or to replenish the diet of released chimpanzees (Hladik 1973, 1974, Wrangham 1977, Baldwin *et al.* 1982, Goodall 1986).

Wrangham (1974) observed how the reduction of provisioned food for the chimpanzees in Gombe, Tanzania, increased chimpanzee aggregation size at the feeding site and increased aggression between the chimpanzees waiting for and feeding on the bananas as well as between chimpanzees and baboons also present at the feeding station. The author concludes that this increased aggression might be partly responsible for the fact that chimpanzees hunt and feed on baboons at Gombe (Wrangham 1974).

Furthermore, Wrangham (1974) suggests that the provisioning of food could also affect the area used and the size of the observed chimpanzee population at Gombe. A view that is also supported by Baldwin *et al.* (1982) who believe that the provisioning of food artificially decreases the size of the foraging area used by chimpanzees and leads to overestimated density estimates for chimpanzee populations at such study sites.

Feeding techniques

Nishida & Uehara (1983) summarize the feeding techniques of chimpanzees as follows:

Leaves:

Chimpanzees hold the leafy branch with one hand and strip tiny leaves off with the mouth in a stroke of head movement, or pull them through with fingers and put them into the mouth.

Blossoms:

Blossoms are usually eaten in a similar way as the leaves. For some species chimpanzees break off and hold the flowering branch with one hand and put each blossom into the mouth.

Fruits & Seeds:

Fruits and seeds are mainly taken in the tree. However, for some species chimpanzees prefer to eat fallen fruits, rather than intact ones, these are mostly dry fruit types with sticky pulp available in the dry season.

Some adults remain on the ground picking up and feeding from the fruit-laden branches which are inadvertently discarded by conspecifics climbing on the tree. Chimpanzees usually feed on seeds, pulp and fruit-skin from immature fruits, and only seeds from mature fruits of a few species. Hard-shelled fruit are bitten open with incisors.

Pith:

Herbs of Poaceae and Zingiberaceae are eaten quite regularly throughout the year. Usually pith of lower parts of immature grass and mature zinger stems are eaten.

Bark:

Outer and inner bark of some species are consumed.

Wood:

Though rarely, chimpanzees earnestly feed on (sometimes lick on) live or dry wood of particular trees. Some of the dry trees are regularly visited by chimpanzees and huge "caves" are thus formed.

Resin:

Resin is available only in small quantities. Usually a chimpanzee stands bipedally on the ground and picks off a small piece of resin.

Root:

A few species of woody roots which emerge on the ground are cut off with incisors and chewed.

Feeding culture

Chimpanzees select their food items mainly according to availability. Interestingly, however, different chimpanzee communities show differences in food choice: some food species, though equally available to both communities are cherished by the one but ignored by the other (Goodall 1986).

There are a number of examples supporting this statement. For example oil-nut palms (*Elaeis guineensis*) grow at Mahale and at Gombe. While Mahale chimpanzees have never been seen to feed on any part of this plant the chimpanzees at Gombe feed on the fruits, pith, dried flower stems, and dried or rotten wood fibres of oil-nut palms (Nishida *et al.* 1983, Goodall 1986). Furthermore, 16 different foods from nine different plant species, which are present in Mahale and Gombe, are eaten regularly by the Mahale chimpanzees but have not been seen eaten by chimpanzees at Gombe at all or only very seldom (Nishida *et al.* 1983, Goodall 1986). The authors relate these differences in feeding techniques and food choices to different local traditions in the two chimpanzee populations (Nishida *et al.* 1983, Goodall 1986). Table 4.6 gives examples of plants species and fruit eaten by chimpanzees at different study sites.

Table 4.6: *Plant species and fruits eaten by chimpanzees at different study sites*

Plant Family	Plant species	Source & Study Site*
Anacardiaceae	<i>Pseudospondia microcarpa</i>	1,2,3
	<i>Lannea velutina</i>	1
Burseraceae	<i>Canarium schweinfurthii</i>	2
Caesalpiniaceae	<i>Cassia</i> sp.	1
Commelinaceae	<i>Cyanotis lanata</i>	1
Euphorbiaceae	<i>Alchornea cordifolia</i>	2
Mimosaceae	<i>Albizia zygia</i>	2
Moraceae	<i>Ficus exasperata</i>	2,3
	<i>Ficus gnaphalocarpa</i>	1,2
	<i>Ficus vallis-choudae</i>	1,3
Ochnaceae	<i>Lophira alata</i>	1
Papilionaceae	<i>Pterocarpus</i> sp.	2,3
Rubiaceae	<i>Nauclea latifolia</i>	1,2
Zingiberaceae	<i>Aframomum</i> spp.	2,3

- *
 1 = Mount Assirik, Senegal, McGrew *et al.* 1988.
 2 = Bossou, Equatorial Guinea, Sugiyama & Koman 1987.
 3 = Mahale Mountains, Tanzania, Matsumoto-Oda & Hayashi 1999.

Nishida *et al.* (1983) define *culture* as a manner by which animals select one of alternatives. The cultural differences observed in the diet of these non-human primates might originate largely from subtle differences in the environment. Furthermore, a confounding factor in the interpretation of this behaviour might be a difference in the quality of food types, e.g. intraspecific variation in plant chemistry (Nishida *et al.* 1983, Goodall 1986).

It seems that the age class most likely to introduce new feeding habits into a chimpanzee community are the youngsters: they still like to explore and try out different food items, while adult chimpanzees are usually more conservative in their feeding habits (Nishida *et al.* 1983, Goodall 1986).

Chimpanzees as seed dispersers

"Plants of humid tropics depend upon animals for the dispersal of their seeds and fruit is an important food item for many tropical animals" (Estrada & Coates-Estrada 1986). This statement indicates a symbiosis between the tropical rain forest habitat and its frugivorous inhabitants. This mutualism will be elaborated in the following section.

Basic principles of seed dispersal

Hladik & Hladik (1967) distinguish three ways of seed dispersal by trees, namely by water, by wind - which is rare in tropical forests (Janzen 1970) - and by animals. For the latter they define three mechanisms of seed dispersal (Hladik & Hladik 1967):

epizoochory:	a passive transport of seed, e.g. in the fur
synzoochory:	an active transport, e.g. storage of seeds by ants or squirrels
endozoochory:	transport after ingestion, if the seeds which are eventually excreted in the faeces retain their ability to germinate.

Gautier-Hion *et al.* (1985, 1993) divide the "consumer effects on seeds" into three different categories. In their comparison of two African monkeys they define *seed dispersers* as monkeys who eat only the pulp or the aril of seeds and disperse the seeds by epi- or synzoochory. *Predators* are those monkeys who destroy seeds by eating them, and monkeys are regarded as *neutral consumers* when they simply discard the intact seed under the tree where they forage for fruit. However, all seed predators also act as seed dispersers, either for different kinds of seeds or for a certain percentages of the species they prey on (Janzen 1970, Gautier-Hion *et al.* 1985).

Germination success of dispersed seeds

When evaluating the dispersal ability of whole seeds dispersed by endozoochory the main criterion is that the majority of excreted seeds retains its ability to germinate (Hladik & Hladik 1967, Janzen 1969, Takasaki 1983). The germination success of endozoochorous seed is influenced differentially by the passage of the seeds through the gastro-intestinal (GI) tract of seed dispersing animals (Chapman & Chapman 1996): Hladik & Hladik (1967) state a generally favourable influence on the germination of seeds after ingestion and excretion by several primate species in Gabon. The authors also observed a positive effect on seedling growth of *Cercopithecus*-dispersed seeds. These seeds generally germinated earlier and the resulting seedlings grew faster and larger than their controls (Hladik & Hladik 1967).

Takasaki (1983) and Takasaki & Uehara (1984) investigated the fate of chimpanzee (*Pan troglodytes schweinfurthii*)-dispersed seeds in the Mahale Mountains, western Tanzania. The authors collected seeds from chimpanzee faecal samples (faecal seeds) and from ripe fruits fallen to the ground (control) for three tree species and found significantly greater germination for "faecal seeds" than "control seeds". Because of their short study period and other uncertainties Takasaki (1983) and Takasaki & Uehara (1984) simply conclude that seeds of these three tree species "do not lose, and possibly increase germinability through ingestion by chimpanzees" and that "chimpanzees could be their efficient disseminators" (Takasaki 1983, Takasaki & Uehara 1984).

Idani (1986) investigated seed dispersal by pygmy chimpanzees (*Pan paniscus*) at Wamba, Zaïre (now: Democratic Republic of Congo). He used faecal seeds from two bonobo study groups (65 individuals and 80 - 100 individuals) and control seeds from ripe fruits. He found that a number of species showed a significantly higher germination rate for faecal seeds than for control seeds, while other species had a higher germination rate in control seeds than in faecal seeds (Idani 1986).

Wrangham *et al.* (1994a) investigated seed dispersal by forest chimpanzees (*Pan troglodytes*) in the Kibale Forest Reserve, Western Uganda. In the ten fruiting tree species that the authors examined they found that faecal seeds of all species had a higher probability of germinating than control seeds. Control seeds of only two species showed any germination at all (*Tabernaemontana* species and *Ficus* species). Furthermore, the time to germination of faecal seeds was shorter than that of control seeds (Wrangham *et al.* 1994a).

Therefore, seed dispersal by endozoochory in many cases has a positive effect on the onset, speed and success of germination. In some cases it has no effect on the excreted seeds' performance and occasionally it might even prevent or reduce the germination success.

The significance of seed dispersal

Janzen (1969) stresses the "escape component" of seed dispersal. Dispersal can be achieved by gravity, water, wind, but in forests is most effectively achieved by vertebrates. The aim of seed dispersal in this case is to enable the "escape of the offspring of a large sessile organism away from predators and parasites" (Janzen 1969). Janzen (1970) also introduces the concept of *distance-responsive* and *density-responsive predators* for seeds dispersed in close vicinity to the parent tree. While the former predators are mainly parasites on adult trees, they act as predators of the young seedlings (Janzen 1970). Predation by the latter though, is mainly a function of the ecological distance between a certain juvenile and other juveniles of the same species (Janzen 1970).

Augsburger (1984a+b) tested the *escape hypothesis*, i.e. the hypothesis that dispersal increases the offspring's probability to escape density- and/or distant dependent mortality that might be high near the parent tree. She furthermore established and tested the *colonization hypothesis* which states an increased probability that some offspring might end up in a disturbed site as a result of dispersal. It is assumed that such a disturbed site, e.g. a light-gap in a forest, enhances seedling establishment and survival and that the probability for the occurrence of a gap within the dispersal range of a parent tree increases with increasing dispersal distance (Augsburger 1984a+b). She concludes that pathogen activity greatly influenced the location where seeds and seedlings survived and that the survival of offspring to the seedling stage is expected to occur away from the parent tree. Her findings furthermore suggest that the latter is true for distance- and/or density-dependent mortality of seeds of shade-tolerant tree species (*escape hypothesis*) also in shaded conditions, while in light-gaps (*colonization hypothesis*) it is valid for all of the tree species studied by her in the semi-deciduous lowland forest on Barro Colorado Island, Panama (Augsburger 1984a+b).

Schupp (1988b) found exactly the opposite in his study of seed and early seedling survival also at Barro Colorado Island, Panama. In his study, seed dispersal to tree fall gaps had no effect on seed survival and actually reduced seedling survival. He suggests that the tangle of limbs, lianas and litter in a tree fall gap offers small terrestrial rodents, known seed and seedling predators, a refuge from their own predators. Their impact on seed and seedling predation for a shade-

tolerant tree species would thus be greater in tree fall gaps than in the forest under story (Schupp 1988b). Schupp & Frost (1989) made similar observations in Costa Rica. The results of their study led them to realise that the association between seed dispersal and seed survival is habitat-dependent (Schupp & Frost 1989). Howe (1989) summarizes this effect in a broad sense by saying that "fruit-eating animals deposit viable seeds in patterns that determine the conditions under which seedlings live or die". The post-dispersal fate of a seed indicates whether the fitness of the plant has been raised or lowered through dispersal of the seed by the frugivore (Estrada & Coates-Estrada 1986).

Martínez-Ramos & Alvarez-Buylla (1986) distinguish two different dispersal syndromes depending on the ecological importance of different plant species. In their study site of a wet tropical forest at Los Tuxtlas, Mexico, they observed the recruitment of (1) pioneer (shade-intolerant) and (2) persistent (shade-tolerant) species, the latter of which they divide into upper-canopy tree species and under storey tree species. They found that pioneer trees have the greatest chance to reach maturity in large forest gaps of a size $> 100 \text{ m}^2$ (Martínez-Ramos & Alvarez-Buylla 1986). Both persistent tree types show a spatially more restricted seed dispersal. Their chance of recruitment to maturity is greatest in smaller tree fall gaps of $> 20 \text{ m}^2$. These gaps occur about seven times more often than the larger forest gaps and thus lead to a recruitment wave which is different in time from the one of pioneer tree species (Martínez-Ramos & Alvarez-Buylla 1986).

The authors also formulate a general guideline for the relationship between seed dispersal, gap dependence and fruiting behaviour of tropical trees in that they state that the short-lived and fast growing as well as strongly heliophilic pioneer trees germinate only in forest gaps, have rapidly growing seedlings that mature at an early age and produce fruits which bear a large number of seeds $< 5 \text{ mm}$ long. Thus, these seeds can easily be dispersed by a number of animals of varying size (*opportunists*). Persistent tree species, on the contrary, generally produce relatively small fruits containing large seeds $> 5 \text{ mm}$ long in relatively short reproductive periods of ≤ 3 months (Martínez-Ramos & Alvarez-Buylla 1986). The authors state furthermore that the recruitment of Upper canopy trees depends more on the frequency of gap formation than on the actual gap size. (Martínez-Ramos & Alvarez-Buylla 1986).

For both persistent tree species the authors state that survival and growth rates of pre-reproductive individuals may be increased in gaps (Martínez-Ramos & Alvarez-Buylla 1986). Since the frequency of tree fall incidences and thus of gap formation increases during rainfall this climatic factor also plays a role in determining population size and structure of gap-

dependent tree species (Martínez-Ramos & Alvarez-Buylla 1986). Gap formation is also dependent on the time when an area has last suffered a tree fall: the lowest probability for a gap to occur is in areas younger than ten years or older than 60 years. Whereas the maximum probability for gap formation - through rainfall - exists in areas where the trees are between 30 - 45 years old. This corresponds with the maximum age of the most abundant pioneer tree species (Martínez-Ramos & Alvarez-Buylla 1986).

In summary, for both, pioneer and persistent species the authors conclude that the dispersal pattern found in the adult population is a result of (1) pre-reproductive thinning through mortality due to unfavourable conditions and (2) the spatial pattern of gaps. Thus, the population size of plants is mainly controlled by animal-mediated dispersal patterns and the within and between years, rainfall-induced, tree fall patterns (Martínez-Ramos & Alvarez-Buylla 1986).

Schupp (1993) concentrates on the animal-mediated aspect of plant recruitment and defines *disperser effectiveness* as a way of ranking the usefulness of an animal disperser for the survival of a certain plant species. He defines *disperser effectiveness* as the contribution a disperser makes to the future reproduction of a plant (Schupp 1993). The two components of disperser effectiveness are (1) the quantity of seed dispersed and (2) the quality of dispersal provided to each seed, resulting in the simple equation of $Effectiveness = (Quantity) \times (Quality)$ (Schupp 1993). Both, quantity and quality are determined by two factors. The quantity of seed dispersed depends (1) on the number of times a disperser visits a plant and (2) on the number of seeds it disperses subsequent to each visit (Schupp 1993). While the quality of seed dispersal depends (1) on the kind of treatment the seed receives in the mouth and in the gut of a disperser and (2) on the quality of seed disposition, i.e. the probability that the seed will survive and become an adult (Schupp 1993). Schupp (1993) concludes that further studies of effectiveness are necessary and should mainly focus on the consequences of dispersal by different disperser species, which should combine the studies of behaviour, morphology and physiology of disperser species with studies of the demography of plants (Schupp 1993).

Who disperses seeds?

According to White (1994a) frugivores are the dominant group of vertebrates in the forest, while mammals (flying and non-flying) are the most abundant of these frugivores and constitute together with various species of birds an array of dispersers that provides considerable mobility to the seeds they ingest (Martínez-Ramos & Alvarez-Buylla 1986).

Gautier-Hion *et al.* (1985) distinguish two main classes of seed dispersers, based on the kind of fruits they mainly forage. They determined the existence of a *bird-monkey syndrome* (Coates-Estrada *et al.* 1993) and a *ruminant-rodent syndrome*, combining taxa that feed mainly on a certain type of fruit. They observed a number of fruit consumers, but of those only classified birds and monkeys as true dispersers, while all other species are classified as mainly *seed predators* (Gautier-Hion *et al.* 1985).

Terborgh (1986) calculated that those mammals and birds that mainly feed on the reproductive parts of plants make up a biomass of about 1 400 kg/km² of mammals and 160 kg/km² of birds in an undisturbed Amazonian locality in south eastern Peru. In their order of importance they could be ranked as primates, rodents and peccaries for the mammals and as cracids, tinamous and toucans for the birds. Furthermore, the group could be divided into *pulp-eaters* which feed mainly in trees and make up two thirds of the biomass, and into *seed predators* which feed mainly on the ground and make up the remaining one third of the biomass (Terborgh 1986). Of the mammalian biomass about 80% is made up by frugivores. And in this ecosystem over half of this biomass is contained in the population of only six species, the two most prominent being monkeys (Terborgh 1986). The major difference between New World and Old World monkeys lies in the action of folivory, since nearly all Old World monkeys include > 10% leaves in their diets (Terborgh 1986). The author describes the importance of primates in tropical forest ecosystems worldwide as follows: "primates occupy a wide range of trophic roles and contribute more to the total biomass of many tropical forest ecosystems than any other taxonomic group" (Terborgh 1986). The validity of this statement is underlined by the number of studies on different species of New and Old World primates and their role as frugivorous seed dispersers (Table 4.7).

Table 4.7: *Primate species and study sites on the trophic role of primates in tropical forest ecosystems*

Species	Locality	Reference
Howling monkey	Mexico	1
Howling monkey & Spider monkey	Peru	2
Spider monkey, Howling monkey & Cebus monkey	Costa Rica	3
Northern bearded saki	Suriname	4
Vervet monkey & Bush baby	Gabon	5
Vervet monkey	Kenya, Uganda & Tanzania	6
Bonobo	Zaire	7
Vervet monkey	Zaire	8
Western lowland gorilla	Gabon	9
Western lowland gorilla	Gabon	10

- 1 Estrada & Coates-Estrada 1986
- 2 Terborgh 1986
- 3 Chapman 1989
- 4 Van Roosmalen *et al.* 1988
- 5 Hladik & Hladik 1967
- 6 Struhsaker 1967
- 7 Idani 1986
- 8 Gautier-Hion *et al.* 1993
- 9 Tutin *et al.* 1991a
- 10 Voysey *et al.* 1999a+b

Concerning chimpanzees as seed dispersers Takasaki (1983) and Takasaki & Uehara (1984) made some observations on the fate of seeds ingested and excreted by *Pan troglodytes schweinfurthii* in the Kasoje area of the Mahale Mountains in western Tanzania. For the majority of the plants studied, viable seeds were passed by the chimpanzees and seed germinability was often increased following their passage through a chimpanzee's gastro-intestinal tract (Takasaki 1983, Takasaki & Uehara 1984). Also important is the fact that many of the fruit plants disseminated by chimpanzees are those utilized by chimpanzees (Takasaki 1983, Takasaki & Uehara 1984). Chimpanzees are efficient disseminators for those seeds and seem to hold a key position in influencing the structure of regional vegetation, especially also since they have a large ranging area and thus defecate part of the seeds far away from the parent plant (Takasaki 1983, Takasaki & Uehara 1984).

Idani (1986) came to a similar conclusion for bonobos and reported on their important role regarding the succession of the vegetation and thus the vegetation structure of the secondary forest as a whole. He assumes that bonobos are probably the most important seed dispersers in his study area (Idani 1986).

In the Kibale Forest Reserve in Western Uganda, Wrangham *et al.* (1994a) found that 98.5% of all chimpanzee faecal samples investigated contained seeds and that the most prominent of those were fig seeds. They observed that in general the passage of seeds through a chimpanzee's gastro-intestinal tract increased the percentage germination and reduced the time to germination for the ten tree species investigated. The authors conclude that these Kibale chimpanzees play a more significant role in the primary dispersal of seeds in this Forest Reserve than their low numbers and biomass might imply, and thus underline the potential importance of great apes, in general, for the maintenance and regeneration of tropical forests (Wrangham *et al.* 1994a).

How plants attract animal dispersers

Janson (1983) distinguished between two fruit types: (a) protected fruits, where the ripe pulp is protected by a husk, e.g. oranges, and (b) unprotected fruits, where the flexible skin is < 10% of external fruit dimension, e.g. cherries (Janson 1983). He found statistically significant correlations between colour and fruit type as well as between fruit size and fruit type, because unprotected fruits are significantly smaller than protected fruits (Janson 1983). *Type A fruits* were therefore defined as: small red, black, white, blue, or mixed-colour fruits without a husk, and *Type B fruits* as: large, orange, yellow, brown, or green fruits with a husk (Janson

1983).

In their study on fruit characters as a basis of fruit choice and seed dispersal in a lowland evergreen forest on the M'passa plateau, Makokou, Gabon, Gautier-Hion *et al.* (1985) established a different classification for fruiting plants and their frugivores. They chose seven parameters to classify the different fruits, namely (1) colour, (2) protective coat, (3) type of edible tissue (by decreasing water content and increasing fibre content), (4) seed protection, (5) seed number, (6) fruit, and (7) seed mass. By means of multivariate analysis the following seven fruit syndromes were distinguished: (1) *bird fruits*: small, red or purple, unprotected, often dehiscent with arillate seeds; (2) *small rodent fruits*: variable, only tendency towards small size; (3) *squirrel fruits*: dull-coloured, dry fibrous flesh and few seeds, mass unimportant; (4) *large rodent fruits*: fibrous, large, few and well-protected seeds; (5) *ruminant fruits*: heavy, rarely red or purple but mainly brown and yellow and fleshy; (6) *elephant fruits*: large; and (7) *monkey fruits*: brightly coloured, mass from 5 to 50 g, either dehiscent with arillate seeds or succulent fleshy fruits (Gautier-Hion *et al.* 1985). The authors classify these fruit-eaters as: (1) *dispersers*, animals dispersing intact seeds by endo- or synzoochory; (2) *neutral consumers*, animals leaving the seeds intact under the parent tree, and (3) *predators*, animals destroying the seeds (Gautier-Hion *et al.* 1985). According to these categories the authors classify only birds and monkeys as true seed dispersers, while all the other consumers are classified mainly as seed *predators*, only occasionally and accidentally functioning as seed *dispersers* or *neutral consumers* for some of the fruits they eat (Gautier-Hion *et al.* 1985).

Howe (1993) looks at the paradigm on "specialization versus generalisation", i.e. the view that some of the tropical trees only produce fruits adapted for use by a small number of species that ensure reliable seed dispersion, e.g. *Cola lizae* and western lowland gorillas (Tutin *et al.* 1991b), while other tree species offer superabundant fruits of lower nutritional value to attract a high number of *opportunists*, who collectively disperse seeds reliable as well, e.g. the potential use of *Type A fruits* by a large number of frugivores from different taxa (Gautier-Hion *et al.* 1985). Howe (1993) argues that there is neither strong evidence for nor against the correctness of this paradigm, especially since not many studies have yet looked into the relative importance of different dispersal agents for seedling recruitment, i.e. which disperser species is the most successful to ensure the long term survival of a certain tropical tree species (Howe 1993).

Herrera (1986) doubts the short-term coevolutionary development of plants and their dispersers. He bases his argument on the fact that often predictions on interactions between vertebrate-dispersed plants and their seed vectors have not been verified by findings in the field, but that

those findings revealed patterns that departed significantly from the predictions made. Herrera (1986) distinguishes between *selective agents = non-mutualistic frugivores*, and *non-selective agents = the fruiting environment*. For the former he states an important influence especially for invertebrates and pathogens, since these might often cause up to 60% of damaged fruits on an individual tree. He furthermore mentions that the "*potential for an interaction between fleshy fruits and damaging invertebrates and pathogens is older than any observed interaction with current legitimate dispersers*" (Herrera 1986).

In conclusion, one can say foremost that the knowledge and perception about how plants attract seed dispersers is partly still immature and partly contradictory. It seems that fruiting plants have developed certain characteristics, such as colour, size and morphology, to attract a particular group of disperser species. Whereby some plant species attract a large variety of frugivores, even from different taxa, while others have a more restricted disperser spectrum. The fact that a variety of non-mutualistic frugivores and changing environmental factors also influence the future fate of a fruiting plant's offspring make predictions about plant-disperser mutualism and the resulting distribution in space and time of a particular tree species very difficult, if not impossible.

Predispersal seed predation

"Seed predators are those animals that eat and kill seeds" (Janzen 1970). Arboreal seed predation is a specialised form of seed predation and is a relatively widespread primate dietary strategy found among higher primate species in a variety of forest types on three continents" (Van Roosmalen *et al.* 1988).

Even though the main primate seed predator in the Old World is the black colobus monkey (*Colobus satanas*) from Cameroon (Van Roosmalen *et al.* 1988), Tutin *et al.* (1996) report also about predispersal seed predation by chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) on *Diospyros mannii* in the Lopé Reserve in Gabon. Crunched fragments of seeds were found in chimpanzee and gorilla faeces, while some whole seeds were found only in gorilla faeces, indicating a potential role as *seed disperser* not only as *seed predator* for this frugivore on *Diospyros mannii* (Tutin *et al.* 1996). Great apes can thus function as *seed dispersers* as well as *seed predators* for the same and different tree species in the same tropical forest environment.

Van Roosmalen *et al.* (1988) observed that many unripe seeds and fruits contain a number of secondary compounds, e.g. tannins, to at least partly prevent predation of unripe seeds. The

concentration of these secondary compounds reduces while the ripening of the fruit and seed progresses, thus ensuring palatability of ripe fruit for potential seed dispersers. *Diospyros mannii* uses an outer protection of strong and irritant hair to prevent the predation of its unripe seeds to increase the chance for the survival of its offspring (Tutin *et al.* 1996). Therefore, plants often develop more or less successful defence mechanisms against predispersal predation to ensure a sufficient survival of viable offspring and thus a long term survival of their species.

This finding might underline Herrera's (1986) argument that very often it is the influence of *non-mutualistic frugivores* which is of evolutionary importance for the development of certain plant and fruit characteristics.

Postdispersal seed predation

"The vertebrate-dispersed seed that has survived the voyage through its dispersal agent is usually subject to postdispersal seed predation" (Janzen 1982). This form of seed predation has a major influence on the survival of a tree population (Willson & Whelan 1990).

Janzen (1986) states that the *initial seed shadow* of an individual tree is dependent on the species of large mammal that produces it. This shadow is differentially thinned and trimmed by post-dispersal seed predation into a *final seed shadow*. After germination of the seeds an *initial seedling shadow* is created which might again be thinned and trimmed into a *final seedling shadow* (Janzen 1982, 1986). This process is dependent on what kind of seeds are being dispersed by what kind of animal and where. Eventually, all these processes determine the probability of appearance of a new adult tree at a certain location, since this successful appearance is dependent on the number and the temporal distribution of seedling attempts made at a given site (Janzen 1982, 1986).

Schupp (1988a) looked at factors that influence post-dispersal seed survival of the subcanopy tree *Faramea occidentalis* on Barro Colorado Island, Panama. He observed that for *Faramea occidentalis* the survival of seeds was significantly lower in tree fall gaps than in the forest under story. Furthermore, the size of the nearest adult had a complex effect on seed survival: for seeds directly beneath a parent tree survival decreased with increasing size of the parent tree; while for seeds away from a parent tree the size of the conspecific adult had no influence on seed survival (Schupp 1988a). Schupp (1988a) also found that the distance away from an adult conspecific did not directly influence seed survival; neither did the quantity of leaf litter present, nor the proximity to a tree trunk or log. When Schupp (1988a) compared the data for all four years of his

study he found that the above stated pattern repeated itself from year to year, but the location of surviving seeds changed between transects. A transect with a high seed survival in one year did not necessarily show high seed survival also in the following year. It was thus not possible to make predictions about seed survival in a given area for a given year (Schupp 1988a).

Willson & Whelan (1990) evaluated postdispersal seed survival in two habitats (wooded and non-wooded) over three years in Champaign and Vermillion counties, east-central Illinois. The authors found that large depots of seeds were more likely to be discovered by seed predators than small seed depots. Nevertheless, the probability of seed survival was still higher in the larger depots (Willson & Whelan 1990). A finding that is contradictory to the one reported by Janzen (1982, 1986) for guanacaste seeds. Also Willson & Whelan (1990) realized that the spatial and temporal pattern of seed survival is generally unpredictable.

Chapman & Chapman (1996) studied seed and seedling survival of six different tree species over three years in the Kibale National Park, western Uganda. The authors found that, for both, dispersed and non-dispersed seeds there was a bimodal pattern of disappearance that varied between species and locations (Chapman & Chapman 1996). In another study on the fate of dispersed seed in Santa Rosa National Park, Costa Rica, Chapman (1989) found that 51.8% of all seeds disappeared from primate *pseudodefecations* within five days after having been placed in the forest. The seeds were either killed or removed by secondary seed dispersers while the rate of removal varied depending on the seed species (Chapman 1989).

In summary, postdispersal seed predation seems to be an ever changing interaction between the environment (e.g. moonlight patterns, rainfall), the seed predator (e.g. ranging pattern or predator density), the fruiting tree species (e.g. seed size or seed density), and the dispersal agent (e.g. amount of dung, seed density in the dung, dung disperser species).

From the above mentioned studies no definite pattern emerges that would constitute a guideline for the reliable prediction of population dynamics of certain tropical fruiting tree species which are subject to seed dispersal and/or (pre- and/or postdispersal) seed predation.

Seedling survival

"Adult plant dispersion results from an interaction of seed distribution and seed and seedling survival...The varying probabilities of survival for different seed and seedling species, coupled with varying initial seed densities, promote a virtually infinite array of likely relationships between

seed and adult distributions" (Howe 1989).

Augspurger (1984b) looked at the light requirements of seedlings from 18 wind-dispersed neotropical tree species on Barro Colorado Island, Panama. The survival in the sun was positively related with survival in the shade, i.e. seedlings with a high mortality rate in the sun also showed a high mortality rate in the shade (Augspurger 1984b). Depending on their light requirements, seedling survival in the shade fitted a negative exponential model thus indicating that a species-specific constant proportion of individuals die during each time period (Augspurger 1984b). Furthermore, shade tolerance and the proportion of seedlings dying from pathogens and disease in the shade were negatively related, with the lowest disease-induced mortality in the most shade tolerant seedling species (Augspurger 1984b). Augspurger (1984b) concluded that for the seeds of the studied tree species dispersal in space is an important strategy to encounter a more favourable light regime. Since the light requirements of the seedlings changed over time for the different species, the encountered light regime also has implications for the size-age structure of the different tree species. While shade-intolerant seeds often build seed banks and stay dormant until a light gap opens, therefore while some seedlings are able to show restricted growth also in the forest under story, other species have to rely on favourable light conditions in light gaps to be able to germinate and grow (Augspurger 1984b).

In a second study on dispersal and light requirements of seeds from tropical trees in Barro Colorado Island, Panama, Augspurger (1984a) found many of her above stated results replicated. She again found a high mortality among seeds and seedlings due to pathogens under shaded conditions. This mortality was mainly due to fungal infection and for most species was distance-dependant. It was higher close to adult conspecifics than further away from them. Mortality in the shade also varied considerably between species which might again have been due to a difference in shade tolerance (Augspurger 1984a+b).

Augspurger (1984b) also measured the one-year survival for the seedlings of her studied tree species in the sun and in the shade. Augspurger (1984a) concludes from her findings that not only the survival probabilities determine in which location a large amount of seedling recruitment will occur. The number of recruited adults also depends on the original distribution of dispersed and germinated seeds and on the relative survival probabilities of seeds and seedlings at various distances away from their parent trees. Furthermore, seedling distributions might start to vary from the originally seed distributions over time, in case of distance- and/or density-dependent mortality (Augspurger 1984a). This finding might be compared to the seed and seedling shadow thinning and trimming suggested by Janzen (1986).

Popma & Bongers (1988) evaluated the effect of canopy gaps on seedling growth and morphology in the tropical rain forest environment around Los Tuxtlas, Vera Cruz, Mexico. Like Augspurger (1984b), Popma & Bongers (1988) found that all species grew faster and larger in light gaps than in the shade with the effect being even more pronounced in large canopy gaps than in small canopy gaps. Furthermore, dry mass and stem diameter for all species were largest in large canopy gaps and smallest in forest under story (Popma & Bongers 1988). The authors observed that all studied plant species showed a complex growth response. In some aspects they resembled the shade tolerant extreme, in other aspects the shade intolerant extreme (Popma & Bongers 1988). The authors state that it might be possible for a plant to change its growth response during its development in so far that juveniles and saplings might be responding to gaps differently than seedlings do (Popma & Bongers 1988). Popma & Bongers (1988) thus conclude that a differentiation in seedling growth in different forest micro habitats might be the reason for a differentiation in distribution patterns (spatial and temporal) of the plant species involved.

Howe (1989) investigated the demographic effects of deposition patterns on seed and seedling survival. He differentiates between *scatter-dispersed plant species* and *clump-dispersed plant species*. The former are dispersed by small-sized frugivores such as birds or bats. These dispersers regurgitate, defecate or drop seeds singly or in pairs, resulting in the recruitment of isolated individuals (Howe 1989). The latter are dispersed by larger terrestrial or arboreal frugivores who defecate seeds in masses thus producing bouquets of seedlings (Howe 1989). Even though *clump-dispersed* seeds occur in large numbers in close spatial proximity Howe (1989) states that in general only one adult plant emerges from each clump, unless some seeds have been scattered by *secondary dispersal* and consequently also reached maturity.

Even though the author gives several examples to consolidate his hypotheses, he eventually also comes to the disappointingly general conclusion that predictions on seed and seedling survival are hardly possible (Howe 1989).

De Steven & Wright (2002) looked into the recruitment pattern and their population consequences for three canopy tree species over a five-year period on Barro Colorado Island, Panama. All three species were shade-tolerant, animal dispersed and had a relatively rapid germination rate. De Steven & Wright (2002) found that for all three species the annual survival rates increased with plant age and plant size. Thus, recruitment probability increased with plant size, i.e. only a few seedlings survived to become saplings, but a greater percentage of saplings survived to proceed to the next size class (De Steven & Wright 2002). The authors also detected

that the three, apparently rather similar species, showed large differences in seedling and sapling recruitment which he concludes to be directional and not stochastic and which were consistent with recently-observed population trends (De Steven & Wright 2002).

Chapman & Chapman (1996) evaluated the germination of seeds from six different tree species in the Kibale Forest Reserve, western Uganda. For seeds placed along transects they found that only six out of 3170 seeds (0.2%) germinated, while none of the seeds placed underneath parent trees germinated (Chapman & Chapman 1996). For seedlings planted along transects the authors found an average mortality of 30% with a range from 9 - 38% between the different species. Mortality rates under conspecifics and along transects varied between species (Chapman & Chapman 1996). Chapman & Chapman (1996) also looked at seedling damage over a 24-month period. They found that > 50% of the leaves of seedlings from different tree species showed insect damage. Depending on tree species, between 0 to 11% of seedlings experienced serious damage due to mammal foraging. The authors found that an increasing level of leaf damage was related with a decrease in growth rate (Chapman & Chapman 1996).

The latter two articles indicate that the survival rate for seeds and seedlings is extremely small and that the number of mature trees that a parent tree produces per fruiting period might often be as little as ≤ 1 .

After all - how important are chimpanzees as seed dispersers?

"The chimpanzee, which has a diverse food habit and an extraordinary large ranging area, seems to occupy the key position in influencing the regional vegetation" (Takasaki 1983).

Primates in general play an important role in the tropical forest vegetation on three different continents (Janzen 1970, Terborgh 1986). In their remaining Old World habitats chimpanzees, who are foremost frugivores, excrete a high number of seeds, often from different tree species, nearly every time they defecate (Wrangham *et al.* 1994a+b). Since they naturally mainly disperse the seeds of those plants they use chimpanzees continuously perpetuate their own food resources and thus their survival (Takasaki 1983, Takasaki & Uehara 1984). They select fruits from a large array of tree species with rather broad characteristics of fruit size, colour and morphology (Janson 1983, Gautier-Hion *et al.* 1985). They are to a large extent responsible for the spatial distribution of a large number of tree species in their particular habitat since they travel distances of 1.6 - 4.5 km per day, often through different vegetation types (Nishida 1977 in Takasaki 1983).

Idani (1986) estimates that pygmy chimpanzees disperse > 500 seeds per day and presumably between 1,500 to 2,000 on average. With daily travel distances of between 0.4 to 6.0 km a wide spatial distribution of seeds in more or less favourable habitats is ensured (Idani 1986).

For some of the seeds they eat chimpanzees might also act as *seed predators*. Yet, for most seeds they disperse the passage through a chimpanzee's digestive system increases germinability (Takasaki 1983, Takasaki & Uehara 1984, Idani 1986, Wrangham *et al.* 1994a+b)

Even if numbers of seeds dispersed daily by each individual chimpanzee in his natural habitat do look quite impressive they are put into perspective by the very low final recruitment rate for each seed species per dung pile. Post dispersal seed and seedling predation, a number of environmental factors and pathogens cause a tremendously high mortality among dispersed seeds (Janzen 1970, 1982, 1986, Augspurger 1984a+b, Janzen 1986, Estrada & Coates-Estrada 1986, Popma & Bongers 1988, Schupp 1988a, Chapman 1989, Wrangham *et al.* 1994a+b, Chapman & Chapman 1996, De Steven & Wright 2002).

If one hence declares chimpanzees to be their own tropical forest habitat architects one must not forget that this spatial creativity is dependent and based upon an undisturbed artistic development in an unrestricted natural environment over a long period of time.