THE NATURAL HISTORY OF THE CHIMPANZEE (*PAN TROGLODYTES VERUS*), AT MT. ASSIRIK, SENEGAL

by

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ABSTRACT

This study examines the natural history of wild chimpanzees (Pan troglodytes verus) in Senegal, West Africa. This western form of chimpanzee is the least studied of the three geographical races. Ecological studies of chimpanzees have been neglected in favour of behavioural investigations. Those studies which have focussed on ecology have often been distorted by unnatural human intervention. Field studies of chimpanzees are reviewed in terms of their length, the extent of disturbance at the site, and the methods involved.

The study area is described: its hot, arid climate and undisturbed state are emphasised. Methods were devised to gain knowledge of the chimpanzees' ecology without interfering with their behaviour or habitat. A detailed description of the types of vegetation is given, and their proportional distribution reveals that there is less forest and woodland at Mt. Assirik than at any other site where chimpanzees have been studied.

Chimpanzees use the types of vegetation differentially and this shows seasonal variation. Forest is most used at the end of the dry season. At other times of the year, extensive use is made of woodland. Grassland is used during the wet season. Data from observations of chimpanzees and their nests is used to estimate the population size, range and density. The total number of chimpanzees at Mt. Assirik is estimated as about 25 to 30, density is reckoned as $0.1/km^2$ and their home range as 250 to $300km^2$.

The chimpanzees appear to be healthy. Many features of social behaviour, described elsewhere, were confirmed for this subspecies. A high proportion of mixed parties was discovered. This is thought to be an adaptation to an area of open vegetation: its distribution of food, water, and the presence of large carnivores.

The chimpanzees are omnivorous. Although mainly frugivorous, they also eat leaves, flowers, seeds, bark, honey, insects and meat. Two species of insect are eaten seasonally, and two types of tool are used to obtain termites and driver ants respectively. Chimpanzees appear to specialise in nocturnal prosimians as mammalian prey.

Nests are examined in detail and found to be similar to those made elsewhere. Preferences for certain species are demonstrated for the first time.

Finally, the results of the study are compared with the cultural ecology of a human hunter-gatherer society, the !Kung San of Southern Africa. The comparison is used as a basis for speculation on the behaviour of the ancestral hominids.

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A nos pieds, la savane,
La brousse et son âme
Avec sa vie intense,
Souvent cachée mais dense.

Des nids de Chimpanzés
Ont été remarqués
Et leur cries entendus
Mais ils ne furent pas vus.

from "Le Mont Assirik" by Alexe Dupuy Coche de la Ferte

Chapter 1.

INTRODUCTION

1. Introduction

Recent evidence has confirmed biochemically that chimpanzees, (Pan troglodytes), are man's closest living relatives (King and Wilson, 1975). This high degree of relatedness makes the species worthy of detailed investigation. Study of the chimpanzee has tended to concentrate on the behaviour of the species; it has a complex social system and advanced cognitive abilities, still not fully explored.

The ecology of wild chimpanzees is less well known but equally as important. Knowledge of the chimpanzee's abilities and adaptation to the environment suggests hypotheses on the activities of subsistence, the social organisation and the abilities of our common ancestors (e.g. Zihlman, 1978): it also encourages us to speculate on the critical differences between hominoid lines that accounted for modern man's emergence. By examining such features as behaviour, social structure, locomotion, diet, the particular environments of primates and the relationships among these features, we can elucidate selective pressures which have operated on man.

The ecology of the chimpanzee should be studied throughout its range for similar reasons to those introduced above, i.e. that differences are just as important as similarities. Chimpanzees exist today in a variety of habitats, from equatorial rain forest (Jones and Sabater Pi, 1971) to Guinea-Sudan savannah (de Bournonville, 1967). They show variation in their behaviour: for example, chimpanzees at Gombe, Tanzania, gather and consume termites by means of tools (Goodall, 1968); the same subspecies of chimpanzee (Pan troglodytes schweinfurthii) at Budongo, Uganda, has not been seen to do so (Reynolds and Reynolds, 1965) although the same species of prey are apparently available to both populations. The ability to compare modes of adaptation across habitats, e.g. feeding strategies and social organisation, might give us further opportunity to test hypotheses on human evolution.

A second reason for the study of chimpanzees throughout their range lies in the interests of conservation of the species: it is essential to know the limiting factors of chimpanzee distribution. These may come from natural geographical barriers, such as major rivers, or climate, or the vegetation, or they may be superimposed by man, e.g., the density of human populations, or the clearing of land for cultivation.

2. Taxonomy and Distribution

Within the range of the chimpanzee there is a need to look at the differences between subspecies of *Pan troglodytes*. Whether the division into subspecies is meaningful or useful is debatable: Reynolds and Luscombe (1971) doubted whether subspecies can be distuished by examining the physical features of specimens. There is a scarcity of morphological data on specimens from known geographical locations: nor are there adequate sets of photographs of each subspecies in the wild, which could be used for categorising facial colouration. There are problems in classifying captive chimpanzees. They are often of unknown origin and may have interbred in captivity: the conditions of captivity may affect body size (Smith *et al.*, 1975) and skin colour (Reynolds and Luscombe, 1971). Finally, some physical features, which have been used to denote subspecies, e.g. facial colouring and relative abundance of hair on the head, change with age (Reynolds and Luscombe, 1971) and there are large individual differences.

The separation into subspecies might still be useful, however, if populations of chimpanzees were geographically separated and were known to have been separated for a long time. Under these circumstances, genetic drift may have taken place and left the isolated populations genetically distinct. The case for distinguishing long-standing, geographically separated populations is reviewed below.

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Schwartz (1934) proposed only one species of chimpanzee; *Pan satyrus*. This had four subspecies, *verus*, *satyrus*, *schweinfurthii* and *paniscus*. The pygmy chimpanzee of Zaire was not given the status of a separate species. Distributions were as follows (see Fig. 1): *verus* spread westwards from the Niger river as far as the Gambia river: *satyrus* spread from the east bank of the Niger southwards to the Congo river, and eastwards to the Ubangi river: *schweinfurthii* extended from the east bank of the Ubangi to Lakes Albert and Victoria. *Pan paniscus* is now accepted as a separate species, and its distribution will not be discussed.

Vandebroek (1958) accepted three subspecies of the species that he termed *troglodytes*: *verus*, *troglodytes* and *schweinfurthii*. Distributions were the same as above but with one important exception. *Pan t. troglodytes* was not confined to the east of the Niger, but was distributed to the west of the river as far as the Dahomey Gap (see Fig. 1). Vandebroek based his distribution on an examination of 1,037 crania of chimpanzees and information that he had received from others. Unfortunately, the sources of the information on distribution are not given, nor is it clear whether or not the crania were of certainly known origin. It is therefore unclear why the distribution of *verus* and *troglodytes* differed from those of Schwartz, in such a significant manner.

Hill (1969) accepted the above subspecies but added *Pan t. koolakamba*, a subspecies which was said to resemble a cross between a chimpanzee and a gorilla. It was supposed to come from central Africa (within the range of *Pan t. troglodytes*). Distributions of *troglodytes* and *schweinfurthii* remained unaltered, but the distribution of *verus* reverted to that of Schwartz (1934), i.e., as far as the west bank of the Niger. Again, the source of information from the field was not given, and there was no discussion of the disagreement between these distributions and those of Vandebroek. *Pan t. koolakamba* is not currently accepted as a subspecies but is subsumed under *Pan t. troglodytes* (Napier and Napier, 1967).

Figure 1. The topographical features that have been used to describe the distribution of Pan troglodytes in Africa.

It appears that the division of *Pan troglodytes* into subspecies is not clear-cut; nor are the distributions established. No thorough, recent survey of the distribution of wild chimpanzees has been carried out which examines the question of subspecies (or zoogeographical races). It would appear that the most commonly accepted subspecies of chimpanzee, *verus*, *troglodytes* and *schweinfurthii*, are now geographically separated by two large rivers: the Niger and the Ubangi (see Fig. 1). It is important to know, however, whether these are permanent, impassable barriers, and if so, how long they have been barriers, before the subspecies can be considered as long-standing, geographically isolated populations. Unfortunately, the relevant information is not available. One important consensus on the distribution of chimpanzees emerges. No chimpanzees occur in the Dahomey Gap, nor is there any evidence that they ever occurred there. The Dahomey Gap seems to be an effective geographical barrier to many species' distributions (Booth, 1958). The *verus* population to the west of the Dahomey Gap seems to be a long-standing, isolated one, and it is the only population of chimpanzees for which there is evidence of isolation, in the absence of comprehensive surveys.

In summary, there is little evidence for distinguishable subspecies of chimpanzee on the basis of morphology. Geographically isolated populations corresponding to the subspecies *troglodytes* and *schweinfurthii* cannot be confirmed. The distribution of *verus*, west of the Dahomey Gap, is an isolated one, and comparison between these chimpanzees and the others to the east is especially important. To avoid confusion when discussing various populations of chimpanzees, the subspecies as listed by Napier and Napier (1967) will be used throughout this work. An amendment must be made to their stated distribution of *Pan t. verus*, however: Napier and Napier (1967) gave the northern limit of this subspecies as 10°N. De Bournonville (1967), Dupuy (1970) and the present study show that the range should be extended to at least 13° N for chimpanzees in Senegal, and possibly as far as 14°N in Mali (Sayer, 1977).

An ecological study of the West African chimpanzee (Pan t. verus) is long overdue (see Ch. 2). Most of the long-term field studies of chimpanzees have taken place in East Africa e.g., Reynolds and Reynolds, 1965; Goodall, 1968, 1975; Itani and Suzuki, 1967; Suzuki, 1969; Nishida and Kawanaka, 1972. One long-term study has taken place in central Africa (Jones and Sabater Pi, 1971) but West Africa has been relatively neglected. The reason for this is unclear: perhaps it is due to less developed tourism, transportation and national parks systems in West Africa.

The choice of West Africa as a region in which to study chimpanzees was therefore significant, but more important was the choice of the site within West Africa, and the principal methods which were to be employed.

3. Possible biasses in ecological studies

A common difficulty in ecological studies is that the relationship between the studied species and its environment is distorted by large-scale human intervention. If this effect could be measured and standardised, the problem would be less serious, because the effect could be isolated in comparative studies of ecology. Unfortunately this is not usually possible because there are too many interacting variables involved.

With particular reference to chimpanzees, the proximity of human habitation is now known to have serious effects on their behaviour. An obvious, direct effect is the hunting of chimpanzees (Rollais, 1959): this may be for meat (Sabater Pi and Groves, 1972), trophies, or the sale of chimpanzees for export (Jones and Sabater Pi, 1971). In these cases, the populations are directly reduced. An indirect effect is the destruction of vegetation in order to clear land for cultivation (Teleki, 1977), or the felling of large trees for timber (Jones and Sabater Pi, 1971). This destroys the cover, the nesting material and the source of food for chimpanzees, causing them tc move or to perish. The planting of crops may offer chimpanzees easy foraging, and can cause not only a change in the ranging patterns, but also altered energy intake similar to that found when an artificial, concentrated food source is introduced during provisioning (Wrangham, 1974). A social effect from an artifically concentrated source of food might be increased competition for the highly desirable but limited food. Feeding on human crops and refuse affects the health of chimpanzees. Jones and Cave (1960) found a high incidence of dental disease in West African chimpanzees that fed regularly on crops and refuse: they also found many individuals surviving into old age, despite poor dental condition. Such chimpanzees were able to eat easily masticated human crops and rubbish, but would not have been able to survive on their former, natural diet. This gives rise to an abnormal demographic profile. Even the mere proximity to human populations and their diseases may threaten the species. Chimpanzees are susceptible to many human illnesses, and probably more so when stressed: Teleki _et al_. (1976) suggested that the high mortality from disease at Gombe, Tanzania, was a result of indirect stress from provisioning combined with the introduction of human diseases. Resident human populations may selectively destroy the fauna of an area. Harding and Strum (1976) noted that the extermination of large carnivores by human beings resulted in the rise in the population of gazelles. Olive baboons (_Papio anubis_) then exploited the upsurge in the ungulate population by hunting and eating them at an increased rate. Gaulin and Kurland (1976) argued further that the destruction of the large carnivores also permitted baboons to spend less time in feeding on low energy foods, so that they were able to spend more time in hunting. The destruction of carnivores existing with chimpanzees could have similar effects since chimpanzees also prey on mammals (Teleki, 1973).

These are some of the obvious effects of proximity to human habitation; there are probably more subtle ones which are not immediately apparent. For example, chimpanzees may congregate in larger numbers at an artificially concentrated food source than they do at natural feeding sites. It is clear, however, that in choosing a site for a study, one must, if possible, avoid areas close to resident human populations and choose areas which have been least disturbed by man.

For the above reasons, we chose to work within a large national park in Senegal, West Africa. The Parc National du Niokolo-Koba covers 8130 km^2 and now has no resident human population except the guards employed by the park authorities (Condamin, 1974).

With the setting up of the park, which began in 1925, villages were gradually cleared out of the area. Even before the park's establishment, these were few in number: the soil is generally rather poor and not favourable to cultivation. Thus the habitat within the park has been little altered from its natural state.

Before our arrival there was evidence that a small number of chimpanzees existed in the park (De Bournonville, 1967; Dupuy, 1970) and it was reported that they were present in the Mt. Assirik region of the park all year round (Dupuy, 1970; Brewer, pers. comm., 1972). This is an interesting population for several reasons: firstly, they occur on the northwestern limit of chimpanzee distribution. There is one mention of chimpanzees further to the north, in Mali: Happold (1973) listed them as occurring in the Parc National de la Boucle de Baoule ($14^{o}N$) and their presence has recently been confirmed by Sayer (1977). Secondly, chimpanzees at Mt. Assirik exist in a belt of savannah (De Bournonville, 1967) and are subjected to large seasonal variation in climate (Dupuy, 1971). There is a rainy season lasting only 5 months during which less than 1000 mm of rain falls, and there is a dry season lasting 7 months in which temperatures rise to $44^{o}C$ (see Ch. 3). These climatic conditions make a demanding habitat for a species which was generally thought of as forest-dwelling.

Mt. Assirik was chosen as the base for the study because it was known to have a chimpanzee population and had permanently flowing water (Brewer, pers. comm., 1972). Chimpanzees had also been reported at certain places along the Gambia River, which flows through the park (Dupuy, 1970) but there were drawbacks in setting up a study there: chimpanzees were not known to be present continuously, and the banks of the Gambia attract tourists during the dry season: Mt. Assirik, on the other hand, is closed to tourists.

This study of the natural history of wild chimpanzees is part of a now larger synecological study of primates at Mt. Assirik: this latter study includes baboons (*Papio papio*), green monkeys (*Cercopithecus aethiops sabaeus*) and patas monkeys (*Erythrocebus patas*). The Stirling African Primate Project began in the Parc National du Niokolo-Koba on February 15th, 1976 and still continues. I spent 13 months in the field, from February, 1976 till March, 1977, then a further period of 3 months the following year, from March until June, 1978. The data presented here were collected jointly by W.C. McGrew, C.E.G. Tutin and myself. The task of finding and studying the chimpanzees in the beginning, as well as maintaining a camp in such a remote area, demanded a full-time, co-operative effort. The choice of a base camp for the project was made following the advice of Stella Brewer, who ran a rehabilitation project for chimpanzees that have spent time in captivity (Brewer, 1978). Her project was based in a camp on the eastern side of Mt. Assirik, 7 km away. Having lived and worked there for several years, Brewer was able to give us invaluable advice on the locations of permanently flowing water, water holes, etc., and knowledge gained from incidental observations of wild chimpanzees.

The methods used in this study developed from basic principles and then practical experience gained later at Mt. Assirik. The aim was to obtain data on the behaviour and ecology of wild chimpanzees by using methods which would cause the minimum of disturbance. Describing the habitat did not present serious problems of disruption: one can observe it and measure features of it without interference. The observation of animal subjects is not so simple. Chimpanzees which do not live in peaceful association with human settlements are initially afraid of man (Goodall, 1965; Reynolds and Reynolds, 1965), and researchers must overcome this problem.

One method is to use hides in order to observe the subjects undetected. This is successful with animals which have a limited or habitual pattern of ranging, such as gibbons or nesting birds, but chimpanzees do not naturally visit the same area daily, nor do they range within a small, limited area. They range widely and this movement may fall into a seasonal pattern, but cannot be predicted on a daily basis. Nissen (1931) attempted to use hides but found them unsuitable. The use of hides from which to observe chimpanzees is only successful when used in conjunction with a lure. The lure for chimpanzees usually takes the form of an abundance of food, usually fruits. Albrecht and Dunnett (1971) applied the method successfully, using citrus fruits and bananas to attract chimpanzees to an open observation area where they could be viewed clearly from hides.

The use of food to attract animals, often termed provisioning, has been used successfully to aid observation of chimpanzees in another way, without hides. By presenting food in closer and closer proximity to the human observer, chimpanzees come to be positively reinforced for contact with the observer. With repeated contacts, they learn that they will not be harmed or threatened by man. This technique has been demonstrated most effectively by Goodall (1968) but has been used successfully by others, e.g., Nishida (1970).

For ethological studies not related to foraging or ranging behaviour, provisioning may not present serious complications. It is not, however, a good method to use in studying the ecology of a species: it directly disturbs the resources of food in an area; and the distribution and gathering of food are central components in an ecological study. The effects of provisioning are difficult to isolate and to measure in an ecological system. Recent criticism of provisioning arose in connection with the feeding behaviour of chimpanzees at Gombe, Tanzania. Chimpanzees there kill and eat mammals (Goodall, 1963). Gaulin and Kurland (1975) argued that the provisioning of chimpanzees at Gombe made preying on vertebrates energetically feasible, and that baboons became frequent prey since they were also attracted to the banana feeding area. They continued to argue that where chimpanzees are not provisioned the rates of meat-eating are low, e.g., in the Kasakati Basin, Tanzania (Suzuki, 1969). Reynolds (1975) considered that the high incidence of baboons as species of prey was a result of increased tension between chimpanzees and baboons due to the provisioning of bananas. De Pelham and Burton (1976) further argued that large intakes of bananas by chimpanzees caused a nutritional imbalance which they rectified by the high consumption of meat. Until there are detailed before-and-after comparisons of the effects of provisioning, it cannot be known to what extent it influences the rate at which chimpanzees prey upon other species. It does seem likely, however, that provisioning at Gombe increased the incidence of baboons as a species of prey due to the increased contact with chimpanzees (Wrangham, 1974; Teleki, 1977). It must certainly have affected foraging behaviour as the intake of energy from bananas was considerable, especially during the peak of provisioning. Indirectly, ranging, social grouping and incidence of aggression were probably altered (Wrangham, 1974). The risk of possible distortion means that provisioning is not suitable for a general study of the natural history of a species, but should be retained for studies of particular aspects of individual behaviour such as maternal behaviour, play, etc.

Accordingly, we planned to habituate the wild chimpanzees at Mt. Assirik to our observations without the aid of provisioning. We aimed to observe the chimpanzees, perhaps from conealment at first, gradually decreasing the distance between us and them. Such a method necessitated a long-term study since habituation without provisioning is a slow process, e.g., Goodall (1965); Reynolds and Reynolds (1965).

An ecological study should last at least through one annual cycle in order to take account of seasonal differences. It is further desirable to maintain a study for at least two years in order to assess any inter-annual variation. Such variation was known to occur with respect to rainfall within the park (Dupuy, 1971). That factor alone amply justified planning a long-term project.

4. Aims

This thesis was intended to examine the behaviour and ecology of wild chimpanzees in the region of Mt. Assirik, Parc National du Niokolo-Koba, Senegal. The emphasis was to be on behaviour. In the first few months, we realised the difficulty of observing closely a wild, and extremely shy population of chimpanzees that ranged over a large area. As a result the aims of this thesis are modest. They are:

1) to establish further details of the natural history of the West African chimpanzee (*Pan troglodytes verus*), following the pioneering, but brief work of Nissen (1931);
2) to compare this population of chimpanzees with those in eastern and central Africa, paying attention to the methods of study that have been used in the past.

Chapter 2.

REVIEW

1. Introduction

A comparative view of chimpanzee ecology may be best drawn from studies which are matched for several important variables; these have been mentioned in the introduction. They include:

a) the extent to which a population has been affected by human interference.

b) the purpose and methods of the study.

c) the duration of the study.

These factors will be borne in mind during the following review. The review will examine only those studies of wild, free-ranging chimpanzees. Important information coming from rehabilitation projects e.g. Hladik, (1973) will be discussed in the following chapters. The studies are grouped by subspecies, and most space is given to the West African chimpanzee.

Within these categories, they are grouped by roughly comparable habitat types. Habitats are grouped into forest, savanna and mosaic types of vegetation.

2. Pan t. schweinfurthii

The eastern or long-haired chimpanzee is the best studied of the three subspecies, in several different types of habitat. In Uganda, the forest-dwelling chimpanzees have been surveyed several times since 1959. Schaller and Emlen (1963) briefly surveyed chimpanzees during a longer study of the mountain gorilla. The Budongo Forest chimpanzees (see Fig.1) were also surveyed by Itani (1961) and later by Itani and Suzuki, but the Reynolds' were the first to carry out a long-term study. This lasted nine months and examined population density, ranging, feeding, and basic social organisation and behaviour (Reynolds, 1963; Reynolds and Reynolds, 1965). Later Sugiyama came to the same site for a six-month study of social organisation

1. Budongo Forest
2. Gombe National Park
3. Kabogo
4. Kasakati
5. Filabanga
6. Kasoge
7. Rio Muni
8. Mt. Assirik

Figure 1. A map of Africa showing the sites where long-term studies of chimpanzees have been carried out.

and behaviour (Sugiyama, 1968; 1969). He was followed by Suzuki, who completed a seventeen-month ecological study, but he has so far published reports on only specific aspects of this study. Recently Albrecht (1976) described the need for conservation in the area after an 8-month survey of chimpanzee densities in the Budongo and Bwindi forests.

These studies combine to form a comprehensive picture of the behaviour of chimpanzees in the Budongo Forest. The Reynolds' studied unhabituated animals, which were difficult to observe because of their timidity and the dense forest vegetation. They did not provision the chimpanzees, and their results can be considered to be representative of a natural, forest-dwelling population. Sugiyama chose to concentrate on chimpanzees living in an area which bordered a road and lay close to a village. He also attempted, but did not continue to provision them. The chimpanzees became habituated to him and he was able to identify and name 46 individuals. It is unclear from the reports, how much the chimpanzees' proximity to human beings and the attempted provisioning affected their behaviour. We know little of Suzuki's findings except the cases of meat-eating and cannibalism that he observed, (Suzuki, 1971a) and an urgent need for conservation (Suzuki, 1971b).

Eggeling (1947) gave a full account of the basic ecology of the Budongo Forest. The work thoroughly describes the vegetation, the geology, and topography of the area. Eggeling points out that the climate of Budongo varies considerably within the forest, particularly with respect to rainfall. For comparative purposes it would be useful to have specific information on the areas where chimpanzees were studied, climate, proportion of vegetation types within one chimpanzee community's range, availability of water, seasonal differences in vegetation, distribution of food, etc.

Kortlandt (1962, 1967) studied forest-dwelling Pan troglodytes schweinfurthii for 3-month-periods in Zaire. He conducted experiments involving the presentation of novel objects and foods to wild subjects, and recorded their reactions. The brevity of the studies, and the fact that the subjects were observed as they came to raid fruit plantations means that little was learned of their ecology.

There have been numerous studies of Pan t. schweinfurthii in more open habitats. Goodall (1968, 1975) established in 1960 a long-term field project in the Gombe National Park, north-western Tanzania (see Fig.1) which she and her colleagues have continued since then. The study population exists in a mosaic habitat of gallery forest, open and closed woodland and some grassland. The focus of the project has always been on ethology, and provisioning facilitated habituation and the close-range observation of chimpanzee behaviour. The subjects are individually identified, many kinship relationships are known, and the chimpanzees can be followed by an observer throughout the day. This has resulted in a detailed understanding of the behaviour of an entire community of free-ranging chimpanzees.

Aspects of chimpanzee ecology have been examined at Gombe. Teleki (1973) studied meat-eating by chimpanzees, and how ranging, grouping, habitat usage and other important behaviours are related to environmental factors, (Teleki, 1977). Wrangham (1975) carried out an ecological study which related individual feeding and ranging behaviour, and social structure to specified changes in the environment.

Several features of this site and the methods used, however, suggest that conclusions about chimpanzee ecology may be drawn only with caution. Wrangham (1974) suggests that significant changes in ranging and feeding occurred on account of provisioning: these in turn may have caused changes in social organisation. In addition, this population of chimpanzees has limitations imposed upon its range: on one side there is Lake Tanganyika, while human habitation and clearing for agriculture confines the range on the other three sides. This gives rise to what Teleki

(1977, p.74) termed "the closed ecosystem" at Gombe. A further drawback when comparing Gombe National Park with other chimpanzee habitats is that a detailed description of the vegetation and climate still remains to be published.

A number of Japanese researchers have also worked in Tanzania on long-term studies (over several years) in areas to the south of Gombe. Their aims were to elucidate social behaviour, and to a lesser extent the feeding and ranging of wild chimpanzees. They were particularly interested in the adaptive significance of social organisation in chimpanzees. They worked in a number of different areas, all of which were of savanna or mosaic type, comprising forest, woodland, grassland, bamboo and savanna. The long-term sites, shown on Fig. 1, are at Kabogo Point (Itani and Suzuki, 1967), Kasoge (Nishida, 1970, Nishida and Kawanaka, 1972; Kasakati Basin, (Suzuki 1969) and Filibanga, (Itani and Suzuki 1967; Suzuki, 1969; Kano 1972). The last of these sites is particularly interesting, as it seems to be the most open and dry of them all, (Kano, 1972, p.230) although data were not presented for confirmation. The vegetation of the Kasakati Basin is described in detail (Izawa and Itani, 1966; Suzuki, 1969). Local meteorological data were not given in detail, but the climate of the eastern shore of Lake Tanganyika was described in general. Kano (1972) provided a general summary of chimpanzee distribution and a vegetational description of all the study sites. The Japanese work forms an extensive basis for comparative studies of habitats and chimpanzee behaviour. If Gombe National Park is added, there are five long-term study sites on the eastern shore of Lake Tanganyika, all of which have distinctive environmental characteristics. Behavioural differences have already been noted which may relate to the different environments, e.g. Izawa (1970) described nomadic movements of chimpanzee groups in the Kasakati Basin. Such large annual shifts in chimpanzee range have not been found at Gombe. The chimpanzees studied in these Japanese projects, share their terrain with local peoples but have only rarely been known to be crop raiders

(Kano, 1972). Indirect effects such as cultivation, grass burning and the construction of roads do occur, but it is not clear to what extent these human activities disturb the chimpanzees' ranging and feeding or if they threaten the future of these populations, (Kano, 1972, p.63). Provisioning was attempted at all three sites though it is continued only at Kasoge. At these sites, as at Gombe, the provisioning, the influences of human habitation, and the lack of detailed description of habitat, to some extent limit the conclusions that can be drawn about the ecology of chimpanzees.

3. Pan t. troglodytes

The central African subspecies has been the subject of fewer field studies. From Cameroon, Merfield and Miller (1957, p.64) recorded the observation of tool use by chimpanzees to obtain honey from underground bees' nests. More recently in Cameroon, Gartlan and Struhsaker (1972) surveyed chimpanzees during a larger study of polyspecific associations of anthropoids. The information came from rain forest areas which had been considerably altered by human habitation. The only long-term study was carried out by Jones and Sabater Pi (1971). This took place in Rio Muni (see Fig.1) and lasted 17 months. They compared the ecology of Gorilla g. gorilla with that of Pan t. troglodytes in several rain forest areas, and also found evidence of chimpanzee tool use to obtain termites. (Jones and Sabater Pi, 1969). They described the general climate of the area and gave detailed descriptions of the vegetation and topography of three study sites: Mt. Alen (chimpanzees and gorillas); Abuminzok-Aninzok (gorillas); and Mt. Okoro-Biko (chimpanzees). Their results covered comparative usage of types of vegetation, range, density, and feeding of the two species. At Mt. Alen and Mt. Okoro-Biko, villages were situated along logging roads, and the vegetation at all three sites was depleted to varying degrees by logging activities. Chimpanzees were not provisioned, but were observed after careful tracking. Although there were considerable signs of human interference at these sites, the research laid the groundwork for the ecology of the central African subspecies.

4. <u>Pan t. verus</u>

The West African chimpanzee was the subject of one of the earliest primatological field studies. In 1930, Nissen spent less than three months in the field in French Guinea, but he was able to learn much about the behaviour of wild chimpanzees (Nissen, 1931). He worked in an area of mixed vegetation in the Kambi region (south-western Guinea). The area comprised riverine forest, woodland on hillsides, and other areas of bamboo and grassland. He used no provisioning, but attempted to use hides for observation. These were not successful, and most of his observations were the result of patient trailing, followed by observation from a place of concealment. The area under study has a number of human settlements nearby, and although some data on feeding and nesting behaviour were obtained, in such a short time little could be established of West African chimpanzee ecology.

De Bournonville (1967) carried out another short-term study. In just over three months he surveyed many areas in Guinea, then went north into the Parc National du Niokolo-Koba for three days. He sought information on the distribution of chimpanzees in these areas, and how this related to the various types of vegetation, and to human habitation. Not surprisingly, he found chimpanzee density to be low where human density was high, although the human influence appeared to be more severe in areas of open habitat, such as savanna. Chimpanzees in forest areas seemed to tolerate human presence to a greater degree. In his brief survey of the Niokolo-Koba area, he recorded density for chimpanzees to be in the "none or scarce" category. In the absence of any human settlements, he suggested that the low density was probably due to the scarcity of water in the dry season. He also suggested that this population of chimpanzees may have moved into the park only recently, after its creation as an animal sanctuary. Dupuy (1970) disputed this claim.

As conservateur of the Parc National du Niokolo-Koba, Dupuy had known of the chimpanzees' presence for some time before he published his report. It gave a brief description of chimpanzee habitats in the park, as well as a list of all observations and traces of chimpanzees reported in the park from before 1960. Dupuy claimed that vegetation in the park should favour a higher density of chimpanzees, since much of it matches those areas found by De Bournonville to have medium to high densities in Guinea. Dupuy also concluded that water must be the limiting factor.

All other reports on wild chimpanzees in West Africa are the results of brief visits to the field or are opportunistic observations of some aspects of the chimpanzees' natural history.

Kortlandt and several colleagues carried out a series of experiments and observations on chimpanzees living in an enclosure and on others living in forest and savanna areas in Guinea (Kortlandt, 1965, 1966a; Kortlandt and van Zon, 1967; van Zon and van Orshoven, 1967). The work focussed on chimpanzees' reactions to the sudden appearance of a live, tame leopard and on other occasions, a mechanical, stuffed leopard. Other experiments looked at the responses to novel objects.

Albrecht and Dunnett (1971) conducted similar experiments during a 5-month study of chimpanzee behaviour in Guinea. Observations were made at two sites: Kanka Sili was a citrus fruit plantation surrounded by secondary forest; Bossou was a thickly wooded hill with a clearing. They provisioned both populations and observed them from hides. Data were collected on group size and basic social organisation and behaviour, as well as the results of the experiments. Few observations were made outside the provisioning area, so little was learned of ranging or natural feeding.

Four independent anecdotal reports exist of West African chimpanzees' using stones as tools to smash open nuts or fuits. Savage and Wyman (1844) mentioned that chimpanzees from an area between Liberia and Ivory Coast were known to break open fruits of an unknown species with stones in order to eat the nut inside. (Savage and Wyman, 1844, p.383). Beatty (1951) also recorded tool use by chimpanzees from a forested area in Liberia. Beatty saw an adult male smash a nut by placing it on a stone and striking it with another rock. From the Ivory Coast, Rahm (1972) reported that nuts of the species _Panda oleosa_ were found placed in root hollows; stones of quartzite were beside them. On approaching, the observers had heard the sound of nut smashing, but arrived at the scene to find only the stones with smashed nuts beside them. Struhsaker and Hunkeler (1971) reported similar circumstantial evidence from the same area, as well as another species of fruit, _Coula edulis_ found with sticks beside them.

This review shows that despite the many field projects which have studied the wild chimpanzee, much remains to be learned of their natural history. Even studies intended to be ecological have not always measured the natural behaviour, but instead, behaviour which has been influenced, sometimes substantially, by local inhabitants, or scientists, or both.

Chapter 3.

THE STUDY AREA

1. Introduction

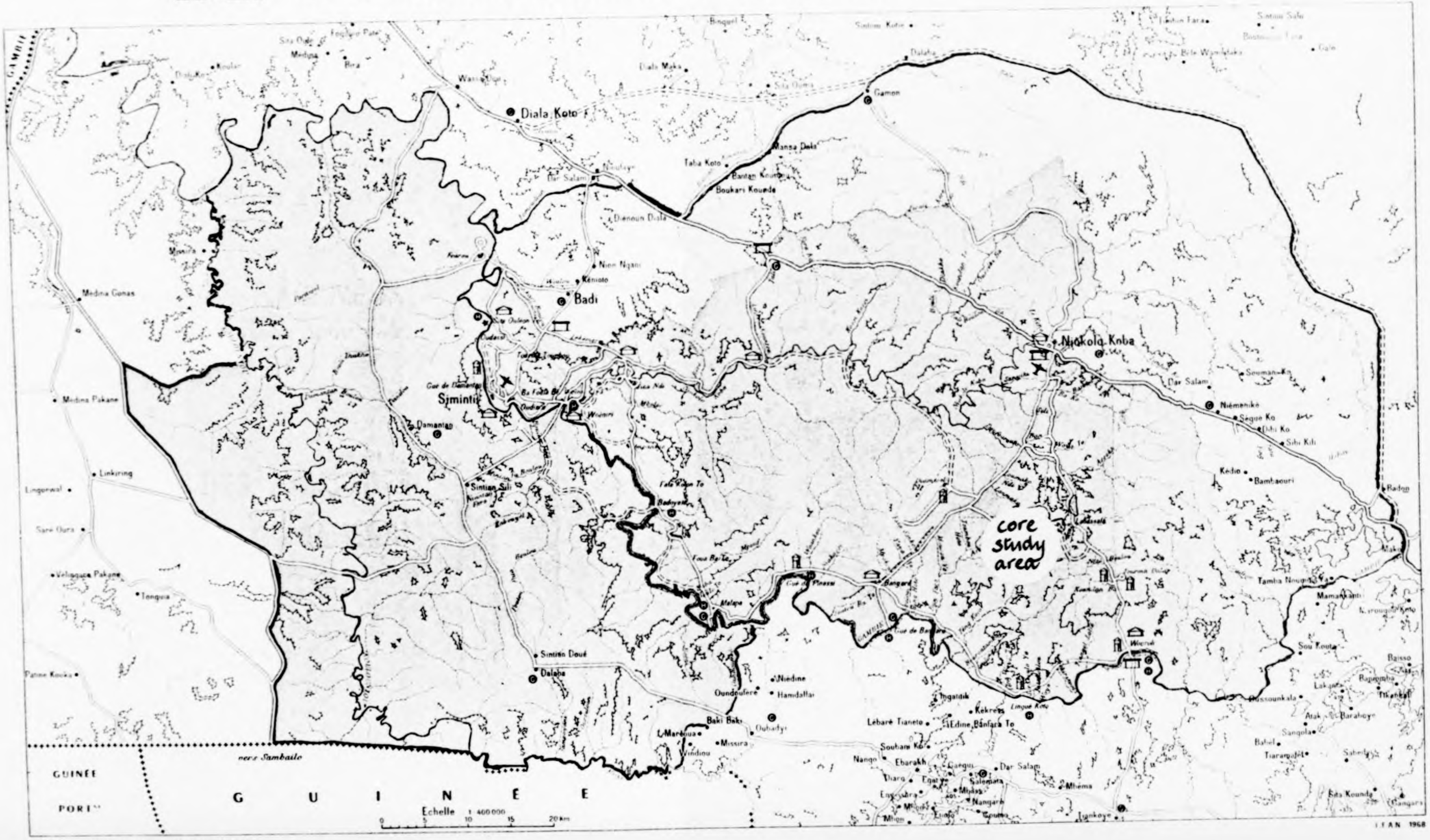
The study area is described in detail because knowledge of its topography, climate and recent history is necessary for understanding certain aspects of chimpanzee behaviour.

2. The Parc National du Niokolo-Koba.

The area in which we worked lies in the Parc National du Niokolo-Koba. This is a large park of 8130km^2, situated to the south-east of the important inland town of Tambacounda (13^{o}N, 13^{o}W). One permanent major river, the Gambia, flows through the park: two other rivers, the Niokolo and the Koulontou provide permanent, though not continuously flowing water (see Fig.1).

The park began its history in 1925 as a small reserve on the left bank of the Koulontou. Gradually other areas were added, either as reserves of flora, or fauna, or both. The region of Mt. Assirik, where this study took place, became a Reserve Partielle de Chasse in 1937. It is not known to what extent hunting took place between this time and 1950, when all hunting was forbidden. A system of surveillance began in 1954 with the creation of the Parc National du Niokolo-Koba. In 1970 the administration of the park became the responsibility of the First Minister in the Senegalese government (Dupuy, 1971). There is a system of guards posted within, and at points on the perimeter of the park. Their function is to prevent poaching and in the tourist season (December - June), to regulate the movements of tourists within the park. The efficiency of the patrol system is helped by a radio network but seriously restricted by the park's shortage of four-wheel-drive vehicles, which are necessary for travel during the rainy season.

Figure 1. The Parc National du Niokolo-Koba with the core study area shown to scale.



3. The Study Area

The area upon which we concentrated lies in the south-eastern part of the park (12°50N, 12°45W): it includes Mt. Assirik and the surrounding district, and covers approximately 50 km^2. This site was chosen for the reasons mentioned in the introductory chapter: chimpanzees were known to occur there; there was permanent drinking water; and it was some distance from the normal tourist routes.

The study area can be thought of as having a 'core' and surrounding areas. The core is an area that we regularly surveyed and examined. Surrounding areas were explored and visited occasionally. The core study area is roughly circular with a radius of 4 km about a centre on the summit plateau of Mt. Assirik. The core study area is described in Chapter 5 when its types of vegetation are defined and measured. Then it is strictly defined as a circle of radius 4 km, giving a surface area of 50 km^2. If the surrounding areas, which we periodically surveyed on foot are included, the area is increased to about 100 km^2. These extensions to the core study area lie in a north-easterly and south-westerly direction from Mt.Assirik.

Mt. Assirik forms the centre of our site (see Fig.2). At 311 metres, it is not a high mountain, but it is the highest point in the park. It has a flat summit plateau with a hard covering of bauxite and little soil (Michel, 1971). The upper slopes of the mountain-side are of scree: broken, crumbling sections of the bauxite covering. These slopes form the catchment areas for numerous seasonal streams as well as the two, permanently flowing streams of the study area: these are Lion Valley to the south-west and Stella's Valley to the east. Lion Valley, viewed from Mt.Assirik is shown in Fig.3).

Some 100 metres below the summit plateau the terrain levels out: there are more plateaux interspersed with areas where erosion has cut into them, forming valleys, in some cases so narrow that they form deep gorges between two expanses of plateaux. Further away from the mountain, these

Figure 2. Mt. Assirik viewed from a lower-lying plateau to the west, in the early dry season.

Figure 3. A view to the west, taken from the summit of Mt. Assirik in the early dry season.

valleys often broaden out, becoming more open and having fine soil from the accumulated alluvial deposits.

The vegetation of the area also varies. This will be discussed in detail in Chapter 5. At this point, a general description is made. On the plateaux, where the soil is thin and poor, the vegetation takes the form of widely-scattered shrubs and trees, generally less than 5 metres high. During the rainy season, and early dry season, there is a covering of grasses. The edge of a plateau marks the beginning of richer soil and correspondingly richer vegetation. This may be an area of grassland or bamboo with scattered tall trees, or else an area of open woodland where trees are much more common: where a plateau is cut by a gorge that retains more moisture, it gives way to gallery forest.

4. Fauna

Since the beginning of this century, both the giraffe (Giraffa camelopardalis peralta) and the topi (Damaliscus k. korrigum) have become extinct in the Parc National du Niokolo-Koba (Dupuy, 1971). The topi was exterminated before the creation of the park, and the number of giraffe probably so much reduced by hunting that the protection came too late. Otherwise the fauna of the area is intact.

A list of all large mammals which have been seen at Mt.Assirik from 1976-1978 can be found in Table I; primates are not included but are discussed separately. A complete list of the fauna for the Parc National du Niokolo-Koba appeared in Dupuy (1971).

Table I shows the frequency with which each species has been seen, and its supposed status with respect to the chimpanzee: potential predator, possible competitor, potential prey and neutral status. Potential predators are the four large canivores: lion (Fig.4), leopard, hyaena and wild dog. We have no evidence that they kill chimpanzees, but chimpanzees give alarm calls whenever lions and leopards vocalise at night. We rarely

TABLE 1. Large mammals (excluding primates) recorded at Mt. Assirik by order of frequency: data from October 1976 to May 1978 inclusive (20 months).

Scientific name	Common name	Frequency	Status
Cephalophus rufilatus	Red-flanked duiker	275	Pot.prey?
* Ourebia ourebi	Oribi	181	Pot.prey?
Tragelaphus scriptus	Bushbuck	140	Pot.prey,rec.
Phacochoerus aethiopicus	Warthog	116	Pot.prey?
Alcelaphus buselaphus	Bubal hartebeest	107	Neutral
Hippotragus equinus	Roan antelope	72	Neutral
Syncerus caffer	African buffalo	69	Neutral
Mungos mungo	Banded mongoose	66	Pot.prey?
Canis adustus	Side-striped jackal	42	Neutral
Loxodonta africana	African elephant	16	Competitor
Herpestes sanguinus	Slender mongoose	11	Pot.prey?
Herpestes ichneumon	Egyptian mongoose	6	Pot.prey?
Hystrix cristata senegalica	Crested porcupine	5	Neutral
Lepus crawshayi	Crawshay's hare	5	Neutral
Viverra civetta	African civet	5	Neutral
* Silvicapra grimmia	Grimm's duiker	3	Pot.prey?
Potamochoerus porcus	Bush-pig	3	Pot.prey,rec.
Panthera pardus	Leopard	3	Pot.predator
Panthera leo	Lion	3	Pot.predator
Lycaon pictus	Wild dog	3	Pot.predator
Crocuta crocuta	Spotted hyaena	2	Pot.predator
Genetta genetta	Common genet	2	Neutral
Atilax paludinosus	March mongoose	2	Pot.prey?
Taurotragus derbianus	Giant eland	2	Neutral
Felis sylvestros libyca	African wild-cat	1	Neutral
+ Heliosciurus gambianus	Gambian sun-squirrel	-	Competitor Pot.prey?
+ Xerus erythropus	Striped ground-squirrel	-	Pot.prey?

* Both these species have been recorded inaccurately: they are difficult to distinguish in the field and it seems likely that oribis have been over-recorded and Grimm's duikers under-recorded.

+ No records of frequencies were kept for small mammals: both these types of squirrel are common.

N.B. In addition, a jackal, thought to be the Common jackal (Canis aureus) was once observed and argument continues as to whether the Bay duiker (Cephalophus dorsalis) is present: observed duikers vary greatly in colouration at Mt.Assirik, yet field guides do not give reliable distinguishing features between the red-flanked duiker and the bay duiker (Dorst and Dandelot, 1972). Neither the common jackal, nor the bay duiker have been recorded for the park (Dupuy, 1971).

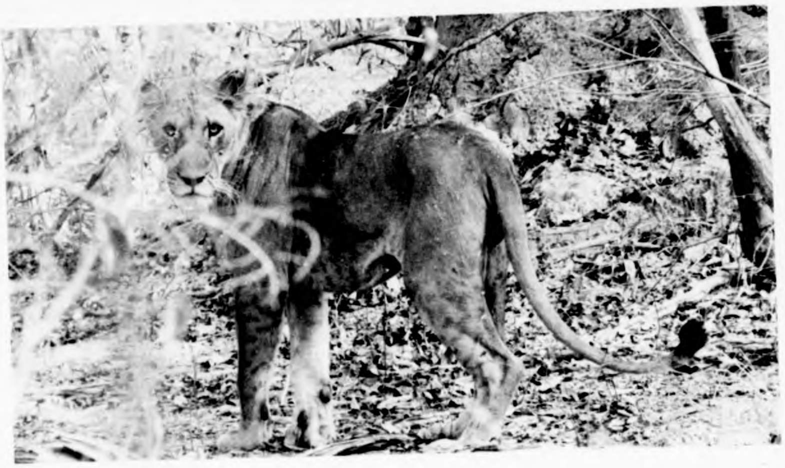


Figure 4. A young adult male lion in grassland.

Figure 5. A bull elephant in woodland.

saw large carnivores, presumably because they are largely nocturnal, but their calls were heard at night. Possible competitors are the other primates and perhaps the elephant (Fig.5); fruit species, e.g., Strychnos sp., which are eaten by chimpanzees, have also been found in elephant dung. The Gambian sun-squirrel (Heliosciurus gambianus) might also compete with chimpanzees since it eats fruits e.g., Pseudospondias microcarpa, which are eaten by chimpanzees. A large number of animals are thought to be neutral, i.e. they do not interact directly with chimpanzees; but there is also an array of potential prey. The only confirmed prey species are the bush baby (Galago senegalensis) and the potto (Perodicticus potto) (see below), but there are a few species present at Mt. Assirik that are eaten by chimpanzees elsewhere (Nishida, 1974; Wrangham, 1975) and several families with forms similar to those eaten elsewhere. Potential prey species, which have already been recorded for other populations of chimpanzees, are labelled (rec), and those similar to known prey species have a question mark beside them.

The other diurnal primates at Mt. Assirik are the Guinea baboon (Papio papio), the green monkey (Cercopithecus sabaeus) (see Figs.6 & 7), and the patas monkey (Erthrocebus patas). Both the closely related vervet monkey (Nishida, 1974) and the baboon (Wrangham, 1975) are prey for other chimpanzees. We have seen no direct interactions between chimpanzees and the other primates, although their diets do overlap to varying degrees. Once in Lion Valley, a mixture of baboon barks and chimpanzee screams was heard with the sounds of crashing among the vegetation: an adolescent female chimpanzee emerged from a thicket and ran along the ground, screaming. She calmed down after a few minutes and rested under a bush, some distance away from the baboons. This may have been an example of direct confrontation over a source of food since they were in an area where an important fruit, for both species, was ripening.

Two species of nocturnal prosimians are present at Mt. Assirik, although

Figure 4. A young adult male lion in grassland.

Figure 5. A bull elephant in woodland.

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Figure 6. Baboons on the edge of a plateau.

Figure 7. Green monkeys on the edge of a plateau.

the evidence is indirect. We have twice seen prosimian eyes in the trees at night on the slopes of Mt. Assirik and two prosimians were observed briefly as they were being consumed by an adult rehabilitated chimpanzee (see Ch. 8). The remains of bush babies and pottos have been found in the faeces of wild chimpanzees. The potto has not been recorded in the park before.

Other animals which are potentially dangerous to at least young chimpanzees, if not adults, also occur. There is a small species of crocodile, (Osteolaemus tetraspis) growing to about 1.5m long, which we have found in four small streams around Mt. Assirik. There are also a number of poisonous snakes. The one most frequently encountered was the puff adder (Bitis bitis) which, although nocturnal, could be found sleeping in the open stony ground during the day. Two species of cobra were also seen (Naja nigricollis and N. haje). Finally, there are also two kinds of scorpion (Pandinus gambiensis and Buthotus hottentota?).

Insects which are important in the diet of chimpanzees will be discussed in Chapter 8 on feeding. Insects which could be classified as environmental hazards were the honey bee (Apis mellifera) and the tsetse fly (Glossina morsitans) occurring at Mt. Assirik. After accidentally disturbing, or even sometimes merely approaching an unseen bees' nest, human beings were attacked most persistently by these bees. The stings could be painful and cause swelling sufficient to incapacitate someone for several days. We were sometimes unlucky enough to pass a bees' nest after chimpanzees had apparently raided it for honey: then the bees were understabdably highly aggressive. The tsetse flies were disturbing because a cloud of them around the head and face made so much noise as to prevent us from hearing animal calls. The bites of the flies were momentarily painful then caused localised irritation.

One hundred and nineteen different species of birds have been identified so far at Mt. Assirik. Their interaction with chimpanzees is thought to be minimal. Even the large birds of prey are unlikely to be dangerous to chimpanzees since infant chimpanzees (the age class vulnerable to birds of prey) are normally in constant proximity, if not contact, with their mothers. Many species of frugivorous birds, e.g., Tockus spp., are likely to compete with chimpanzees for food.

5. Climate

Systematic measurements were made of the climate at Mt. Assirik for two reasons. Firstly, there were no existing meteorological records for the area near Mt. Assirik: the nearest places for which data are available are Tambacounda, about 150km to the north-west, and Kedougou, about 100km to the south-east: the climate differs slightly between these two (Toupet, 1971, p.16). Thus at least some basic description of the climate was necessary. Secondly, measurements in some detail were considered to be important because Mt. Assirik is a marginal habitat for chimpanzees, and some aspects of the climate, e.g. annual rainfull or daily maximum air temperatures, could be critical factors. Indeed Kortlandt (1966) has proposed a "chimpomorphic" habitat with minima of 10°C and maxima of about 25°C.

The climate is characterised by two seasons: the dry season lasts from November until May, and the wet season, from June to October. During the dry season there is rarely a cloud in the sky, although haze occurs when dust and the ashes from bush fires are whipped up into the air by the Saharan wind, the Harmattan, in January and February. During the wet season, although rain does not fall daily, the sky is often overcast.

The general methods for the collection of meteorological data are described in Chapter 4. The results from March 1976 to June 1978 can be seen in Figs. 8 - 11.

Figure 8 shows the mean monthly maxima and minima measured in camp. It can be seen that at the end of the dry season, during the months of March, April and May, the mean maxima rise to about 40°C(104°F) in the shade.

Figure 8. Mean monthly maxima and minima: March 1976 - June 1978, measured in camp.

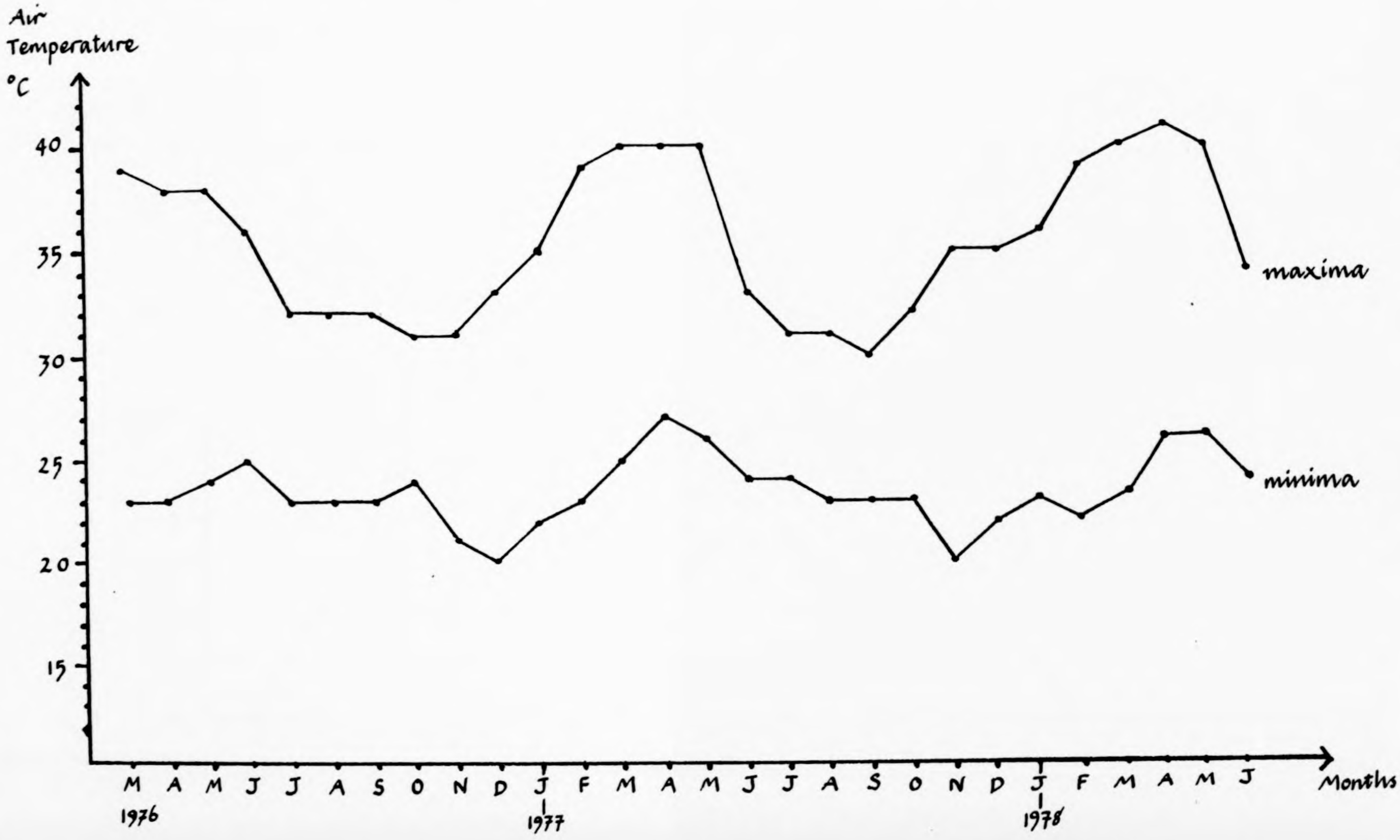


Figure 9. Monthly totals of rainfall: March 1976 - April 1978.

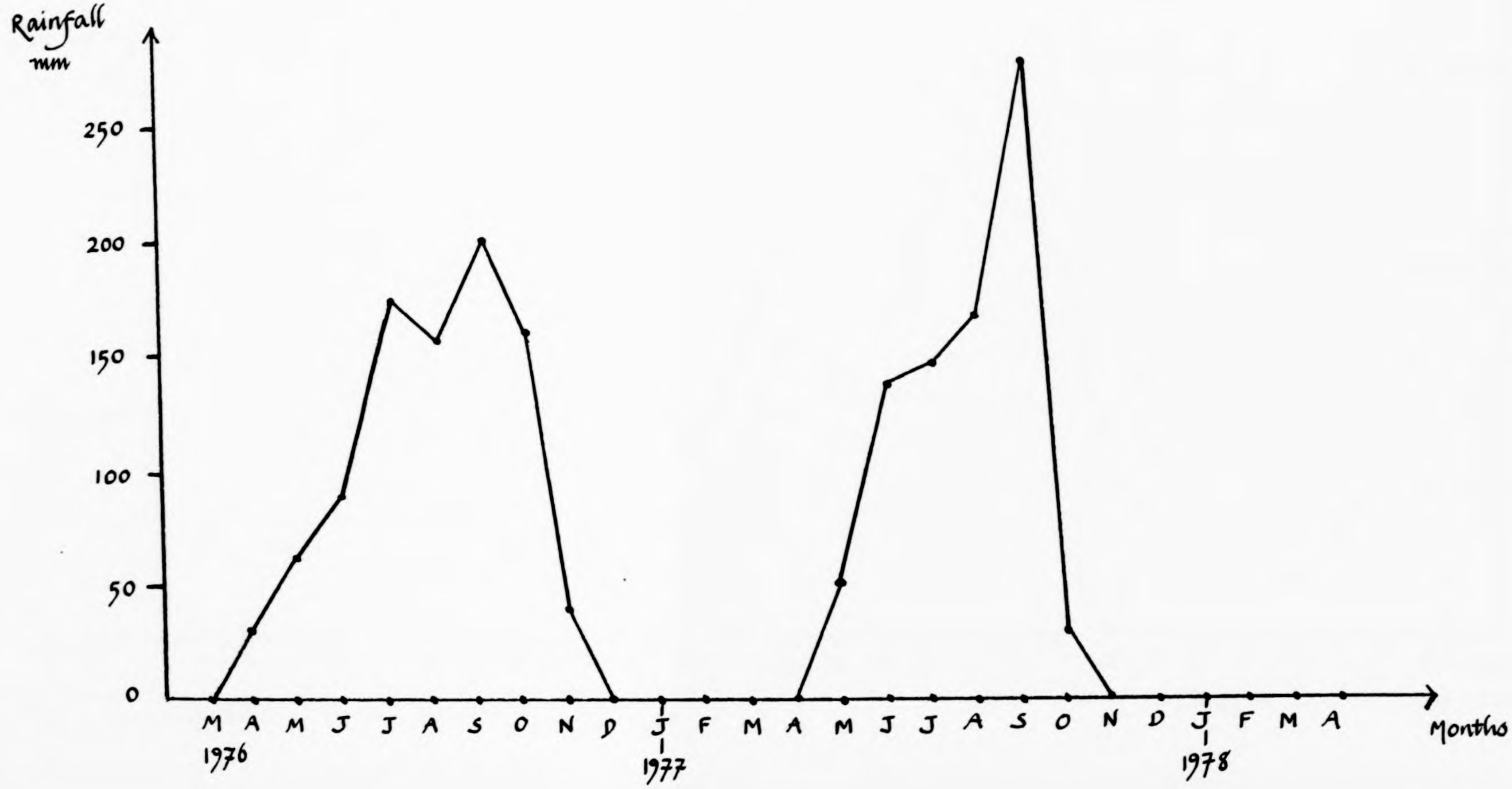
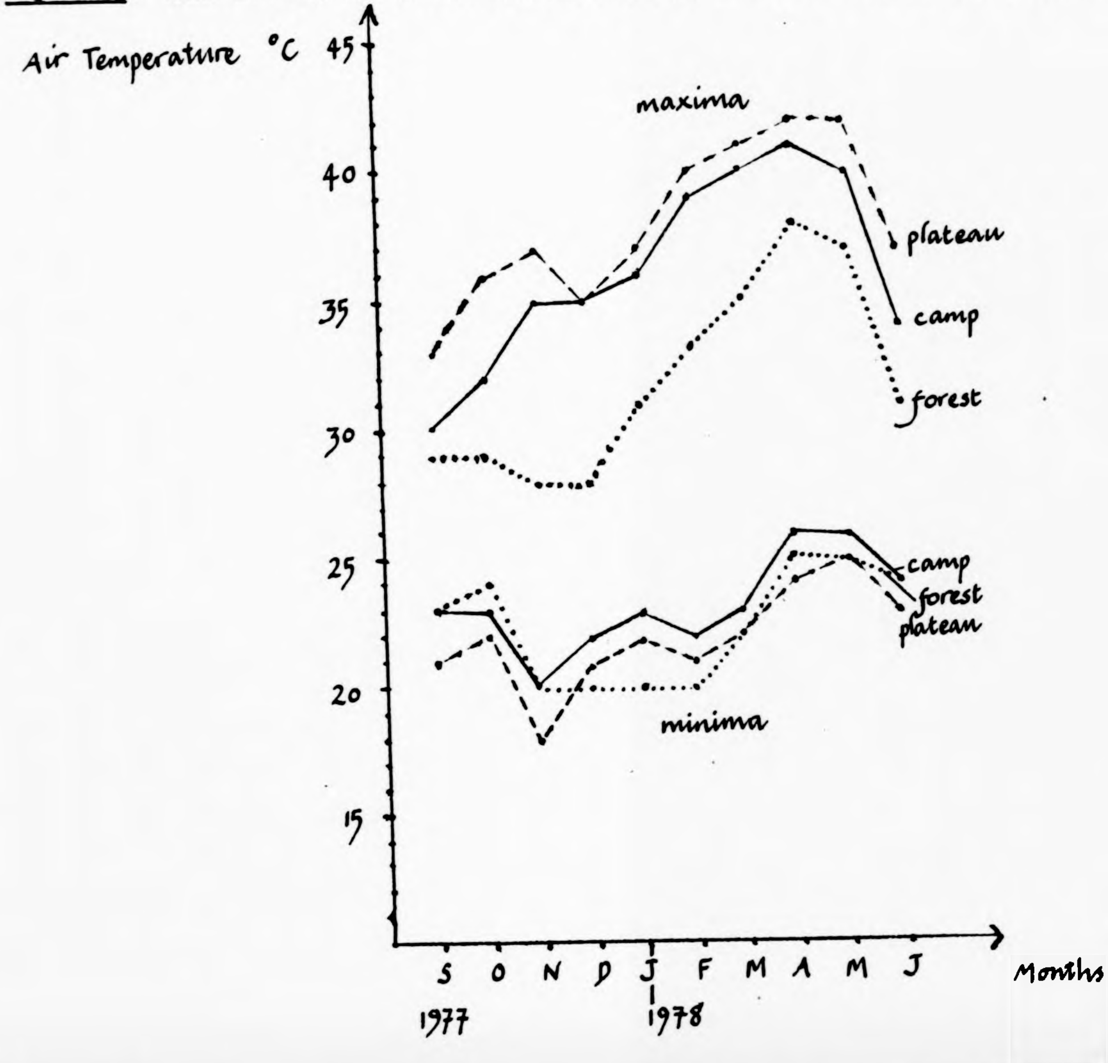


Figure 10. Mean monthly humidities at 0700 and 1600 hours, measured in camp.

Figure 11. Mean monthly maxima and minima in camp, in forest and on the plateau, Sept. 1977 - June 1978.



Mean monthly minima do not fall below 20°C(68°F) at any time of the year. Reference to Fig.11 shows that temperatures measured on the plateau (although still in the shade) are hotter than in camp, with mean maxima rising to 42°C(108°F) at the end of the dry season. By contrast, as Fig.11 shows, the mean maximum temperatures measured in the forest beside the stream bed reveal that it is coolest there: mean maxima rise to only about 38°C(100°F) in April, the hottest month. Camp is situated in a small patch of woodland between the edge of a plateau and the forest (see Fig.12). Forest temperatures, shown on Fig. 11, demonstrate that for most of the dry season the difference between camp and forest temperatures is about 5°C, narrowing to a mean of 3° difference at the end of the dry season. As far as chimpanzees are concerned, these differences in maxima may be important in such a hot climate.

Clearly, these temperatures, even in the gallery forest, indicate that the climate at Mt. Assirik far exceeds the "chimpomorphic" habitat described by Kortlandt (1966b) as being favourable for chimpanzees.

Rainfall totalled 889 mm in the wet season of 1976 and 824 mm in the wet season of 1977. It can be seen in Fig.9 that the rainy season began one month later and ended one month earlier in 1977, compared with 1976. Thus rainfall is not predictable by calendar month, nor it seems, by other seasonal events, e.g., certain fruit seasons. A delay in the onset of rain may be critical for chimpanzees dependent upon residual water at the end of the dry season.

Rain did not fall daily, but usually every few days, with downpours averaging about 10 mm. One day's downpour totalled 43 mm in September, 1976.

Figure 10 shows the mean monthly humidities for 0700 and 1600 hours. These represent the two extremes of humidity during the daylight hours. The humidities naturally follow the pattern of rainfall (Fig.9), with early morning humidity at about 100% in the middle of the wet season. It is also of interest to note that humidities begin to rise in April and May, when

Figure 12. A view of the camp-site, showing its position between plateau on the left, and forest on the right.

Figure 13. One of the five grass and bamboo huts, which form the camp.

maximum air temperatures are at their hottest. This makes the climate uncomfortable. The times of lowest humidity are in the middle of the dry season, about the month of January, when the Harmattan wind blows.

Comparisons are made with other long-term chimpanzee study sites for which some data is available. The results are shown in Table 2. Although it cannot be confirmed until annual rainfalls are measured in the Kasakati Basin, Mt. Assirik appears to be both the hottest and driest of all chimpanzee habitats.

6. The human influence

There are no resident people in the area of Mt. Assirik other than the research team, which numbers four at the most, and a small chimpanzee rehabilitation project, which is situated 7km from our camp. This was founded in 1974 (Brewer, 1978). During most of this study, the rehabilitation project was staffed by three people and involved 6 chimpanzees. The chimpanzees' encounters with wild chimpanzees were few, but ranged from friendly to aggressive (Brewer, 1978). It is Brewer's impression that the wild chimpanzees have decreased their visits to the valley beside her camp since the rehabilitation project began. Unfortunately there are no quantitative records of their presence in the valley from 1974-1976 which could be used for comparison with the present frequency of visits. If the change is genuine, however, it is a serious one, since in an area of little gallery forest (see Ch. 5) the forest of Stella's Valley forms a major contribution. Wild chimpanzees still use it, but there may have been a reduction in the usage.

There are no guards' posts at Mt. Assirik. The nearest ones are at Bangare (15km direct distance) and Wouroli (18km) on the Gambia river to the south, and Niokolo-Koba (15km., direct distance) to the north (see Fig. 1).

The only other human influence in the Mt. Assirik area is occasional poaching. Poachers have been seen twice at Mt. Assirik but evidence of their presence has been found several times. This includes straw around water

TABLE 2. A comparison of meteorological data from 5 sites

Site	Annual rainfall (mm)	Air Temperatures			Source and Comments
		Highest max.	Lowest min.	$\bar{X}$	
Rio Muni	1800 - 3800	33°C	16°C	25°C	Jones and Sabater Pi 1971
Budongo Forest	1780 - 1900	35°C	18°C	25°C	Eggeling, 1947. Air temperatures from Butiaba, outside forest
Gombe	1417	30°C?	19°C?	25°C?	Rainfall, McGrew et al. 1979; Air temperatures Wrangham, 1975.
Kasakati Basin	<1000?	34°C	8°C	22°C	Suzuki 1969
Mt. Assirik	857	44°C	16°C	28°C	Data from two consecutive years

holes to prevent birds from drinking there, cotton thread possibly for the same purpose, nets for trapping birds, small hides made of branches or straw, a snare, a drying rack over the ashes of a fire, bamboo ladders and pegs in the trunks of trees where there are bees' nests (see Fig.14). On the second occasion when poachers were in Lion Valley (April, 1978) we travelled to the guards' post at Niokolo-Koba to inform the authorities. The following morning, guards came to Mt. Assirik and arrested one poacher: he had two large bamboo cages containing small, brightly-coloured birds which were destined for sale and export. A week later the second poacher was arrested. All signs of poaching that we found indicated that it occurred on a small scale, typical of Peul and Bassari people living to the south of the park. There were no signs of any primates being trapped or killed. Historically, the area around Mt. Assirik seems to have been neglected by human beings. A French explorer of the nineteenth century, Dr. André Rançon described this area as being "a complete desert" in 1891 (reported in Dupuy, 1971, p.208).

Of the three tiny villages known to have existed near Mt. Assirik before the creation of the park, only the base stones of a few huts remain, and there is now no discernable difference in the vegetation at these sites compared with nearby areas. It is not known whether these villages were permanent or temporary camps. As far as we can tell, no domestic plants remain.

Our own influence, as resident researchers, was kept as low as possible. Our methods (see Ch. 4) were devised with this purpose in mind. The huts in which we slept and kept stores were unobtrusive (see Fig.13), and only the minimum amount of vegetation was cleared in construction of the huts and making paths. We were also conscious of keeping our level of noise low, in order to enable us to hear animal calls and to minimise our disturbance.

7. The camp-site and living conditions

Figure 14. A poachers' ladder, leading up to a bees' nest in a baobab tree.

Upon arrival, we slept in tents: all other activities took place outside. Three months later we established a more favourable camp-site with bamboo and straw huts as individual sleeping and studying quarters. These proved to be comfortable and convenient. Supplies were bought once every 4 - 6 weeks in Tambacounda and carried by Land Rover to camp.

We cooked over an open fire and baked bread in a stone, wood-fired oven: there was an abundance of dead wood to furnish us with fuel. We ate, read and carried out camp-based scientific activities in a communal, open-air area.

The camp-site lay on a laterite shelf just between a large plateau and a steep-sided section of Lion Valley. Water for cooking and drinking was carried from the stream in the valley up to the camp. We bathed and washed clothes in the stream.

Almost all refuse from the camp was taken to Niokolo-Koba where there was an official tip: small amounts were burned and buried near camp.

8. The population of chimpanzees

The question of the size and range of this population will be discussed in Chapter 6, but mention should be made here of what little has been reported on the history of the population. As Fig. 1 shows the Mt. Assirik area lies near the southern border of the park which at that point is bounded by the Gambia river. While chimpanzees have not been known to occur far to the north of Mt. Assirik, they do occur on the southern side of the Gambia, due south of Mt. Assirik (De Bournonville, 1967). De Bournonville argued that the chimpanzees occurring within the park are recent immigrants, having arrived since the park's creation. According to him, they moved north, crossed the Gambia river, and took refuge in the park because they were hunted by people in areas further to the south. Information obtained from a local person during our study indicates that although baboons are hunted by the Bassari people for meat, chimpanzees are not, being considered too human-like. Dupuy (1970) disputed the claim that the population is a recent addition on the grounds that there were local words for chimpanzee among people living within the park when it was established. Neither claim can be substantiated. The question of the chimpanzees' history is of great interest, since it is not known whether they are part of a continuous distribution, or are an isolated, relict population. It is not known whether chimpanzees cross the Gambia river, but they have not been studied along its banks. Certainly, in the dry season, there are several places due south of Mt. Assirik where human beings can step across by means of exposed rocks, and it seems likely that chimpanzees could do the same. Reports from early explorers suggest that chimpanzees were not common in Senegal and Gambia in recent centuries. Mungo Park travelled up the Gambia river in 1795 but did not report chimpanzees, although he mentioned other animals (Park, 1822). Rochebrune (1883), in a report on the fauna of Senegambia, wrote that chimpanzees were very rare. The only chimpanzee he saw was a young one for sale in a coastal town: the vendor claimed that it came from Casamance - a forested region in south-western Senegal.

If chimpanzees have moved north to Mt. Assirik recently, because of persecution, then one might expect a growth in the population; but a limiting factor to an expanding population at Mt. Assirik may come from the physical environment, e.g., the open vegetation and the scarcity of water.

Chimpanzees have not been found any further north of the Mt. Assirik area, with the exception of rare sightings at Niokolo and the sporadic observations near Simenti, 15km further north, but 50km west (Dupuy, 1970). Observations at the latter site, however, have ceased in recent years. It seems likely that areas to the north do not have an adequate distribution of forest and woodland (i.e., areas of these types of vegetation which are large enough and close enough together), nor an adequate distribution of water to provide chimpanzees with a suitable habitat.

Chapter 4. METHODS AND MATERIALS

1. Introduction

Our general attitude to the methods to be used in the field was that they should cause as little disturbance as possible. The advantage of Mt. Assirik as a site for study was that it was a natural, undisturbed environment, and it was intended to make full use of that fact by keeping it so.

2. Researchers

In view of the risk of passing on human diseases to the primate population at Mt. Assirik, all researchers were immunised against poliomyelitis and tested for tuberculosis. They were also required to have a general medical examination before going to the field.

3. Method for habituation of chimpanzees.

The drawbacks of provisioning to facilitate habituation during the course of an ecological study have been discussed before. To summarise those problems briefly: provisioning is an introduced, artificial distribution of a human crop: this necessarily alters the feeding behaviour of the chimpanzees being studied: in addition, more subtle changes can be caused in the ranging, social behaviour and health of the population.

Instead of provisioning the chimpanzees, it was planned to habituate them to our presence by letting them see us first at a great distance when they would presumably be unafraid, then we would gradually diminish this distance. We assumed that they would become habituated to our observation at ever-decreasing distances and become less timid.

After the first few months at Mt. Assirik, it became clear that the chimpanzees were extremely shy: moreover, they were scarce and ranged widely in the area. For these reasons, the planned habituation would have taken a long time, and during that period chimpanzees would often flee on seeing us, so that our observations would be brief. We changed our strategy and decided to hide ourselves during observation; we attempted to approach chimpanzees to distances as close as 10 metres while remaining concealed.

For this purpose, we wore khaki and green, camouflaged clothing. Long trousers and long-sleeved shirts were worn for maximum camouflage and as protection from the tsetse fly. Observations were made with the aid of Leitz 10 x 40 binoculars. It was usually possible to hide behind foliage: failing a convenient, natural hide, observers crouched on the ground and remained as still as possible: in this way, with the camouflaged dress, we could usually remain unseen for long periods. When chimpanzees moved on, we attempted to follow them without allowing ourselves to be seen. If we lost them or did not see the direction in which they left, we examined the place where they had been observed. At the site, feeding remains and day nests were recorded; faeces were collected for later analysis.

The hours spent in the field were usually from 0730 - 1300 hours in the morning, then 1530 - 1900 hours in the afternoon. This routine allowed us to be in the field during daylight hours, with the exception of the early afternoon period, when air temperatures were highest. During this period, we typed field notes, analysed faecal samples, pressed botanical specimens, etc. Alterations to this routine occurred when a nesting site of chimpanzees was known; occasionally, this meant staying out after dark to locate their nesting site, and arising before dawn, at about 0600 hours, to watch them arise.

Since no domestic staff were employed, researchers took turns in spending a day or half-day in camp to bake bread, cook, wash up, carry water up from the stream, clean equipment etc., as well as taking the hourly readings of air temperature and humidity. This ensured that domestic work was distributed evenly, that researchers had a regular day of comparative rest and solitude, which, in such a small group, proved to be psychologically important.

We worked both singly and in pairs in the field. A morning's search began with a decision to search a given area. This decision was sometimes based on the previous day's sighting of chimpanzees; occasionally, it was just a random choice: Most of the time it was a calculated guess, based on knowledge of fruiting seasons and the current distribution of water.

During searches, observers walked as quietly as possible, constantly listening and looking for chimpanzees. Hand-written notes were taken with ballpoint pen on 'Nalgene' waterproof paper. Other animal sightings as well as nests and all traces of chimpanzees were recorded. If chimpanzees were found, we observed them through binoculars and took notes in as detailed, descriptive manner as possible: their activities were recorded with the minute of their occurrence.

4. Particular methods in detail

4.(i) Nests

The instructions for the collection of these data and a sample card on which this was done are shown in Figs. 1 and 2. The study was designed for comparing nests at Mt. Assirik made in different types of vegetation and during different seasons: its wider application was for comparing nests at Mt. Assirik with those made by chimpanzees elsewhere.

After some months, collection of the data on old and rotting nests (see Fig.1 for definition) was discontinued, because these nests had often disintegrated so much as to render many measurements meaningless.

4.(ii) Identification of plants

Specimens of plants were gathered in duplicate. We ensured that we collected specimens of all species of plants used by chimpanzees as food or nesting material: we also collected specimens of species occurring on transect lines used for sampling the vegetation in different habitats. For each species of plant, a specimen was sent to F.N. Hepper at the Royal Botanical Gardens, Kew for identification.

FIGURE 1.

STIRLING AFRICAN PRIMATE PROJECT - NEST STUDY Key to Nest Cards

Date: Day, month, year
Season: Wet or dry
Location: Named topographical features, e.g., New Valley, Knoll Ridge, etc. (This could be given in habitat type for un-named locations, e.g., gallery forest, open woodland, etc.)
Observer: Name

Tree species: Latin name, or common name.

Tree height: To nearest metre, from base to top of crown.

Lowest branch: To nearest 1m, height of lowest branch from main trunk.

Food/non-Food: If known, is nesting tree being fed upon by chimps at time of nesting.

Nest age: One of 4 categories:
Fresh = Up to 48 hrs. old, intact, all leaves green & still flexible, usually fresh faeces (i.e. still moist) below
Recent = 2-7 days old, intact, leaves still green but dry and brittle, usually dry faecal remnants below
Old = older than 7 days, virtually intact, leaves brown although some on best branches may still be green, no faeces below
Rotting = age varies from approx. 1 month to several months, nest structure disintegrating, leaves often missing or if remaining may be dark brown or black, no faeces below.

Nest Height: to nearest 1m, vertical distance from rim of nest to ground below.
Nest Diam.(l) longest diameter to nearest 10cm.

Nest Diam.(s): shortest diameter to nearest 10cm.

Nest depth: To nearest 10cm distance from rim of nest to bottom of it.

Main Bran.: Number of branches of diameter of 2.5cm or more which form part of the nest.

Open/Closed: To nearest 1m, distances to 3 nearest nests, up to 15m from target nest. Note if these are not same ages.

Others same Tree: Number of other nests in same tree as target nest.

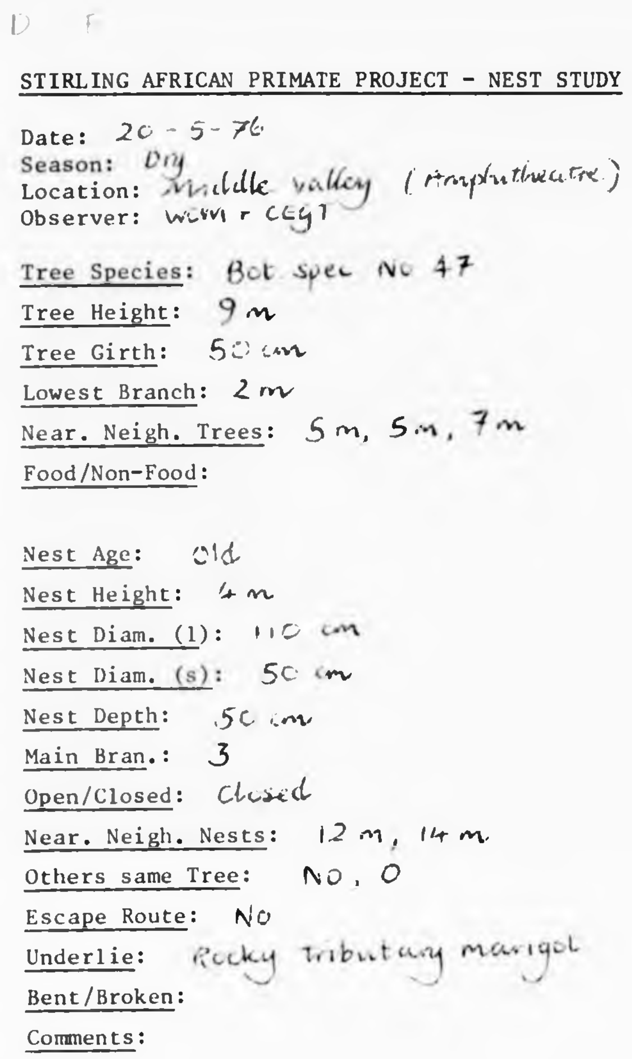
Escape Route: Could chimp move to ground without using trunk(s) of nesting tree?, e.g., into canopy of neighbouring tree.

Underlie: Describe substrate under nest, e.g. streambed, cliff edge; thick grass.

Comments: Is nest part of big group? Does nest have any unusual features? Etc.

Near Neigh.Trees: To nearest 1m, distances to 3 nearest trees from nesting tree, up to 15m away. Tree = at least 5m high.

N.B. If distances are estimates, put (e) after numbers.



D F

STIRLING AFRICAN PRIMATE PROJECT - NEST STUDY

Date: 20 - 5 - 76
Season: Dry
Location: Middle valley (Amphitheatre)
Observer: WCM + CEGT

Tree Species: Bot spec No 47

Tree Height: 9 m

Tree Girth: 50 cm

Lowest Branch: 2 m

Near. Neigh. Trees: 5 m, 5 m, 7 m

Food/Non-Food:

Nest Age: Old

Nest Height: 4 m

Nest Diam. (l): 110 cm

Nest Diam. (s): 50 cm

Nest Depth: .50 cm

Main Bran.: 3

Open/Closed: Closed

Near. Neigh. Nests: 12 m, 14 m.

Others same Tree: NO, 0

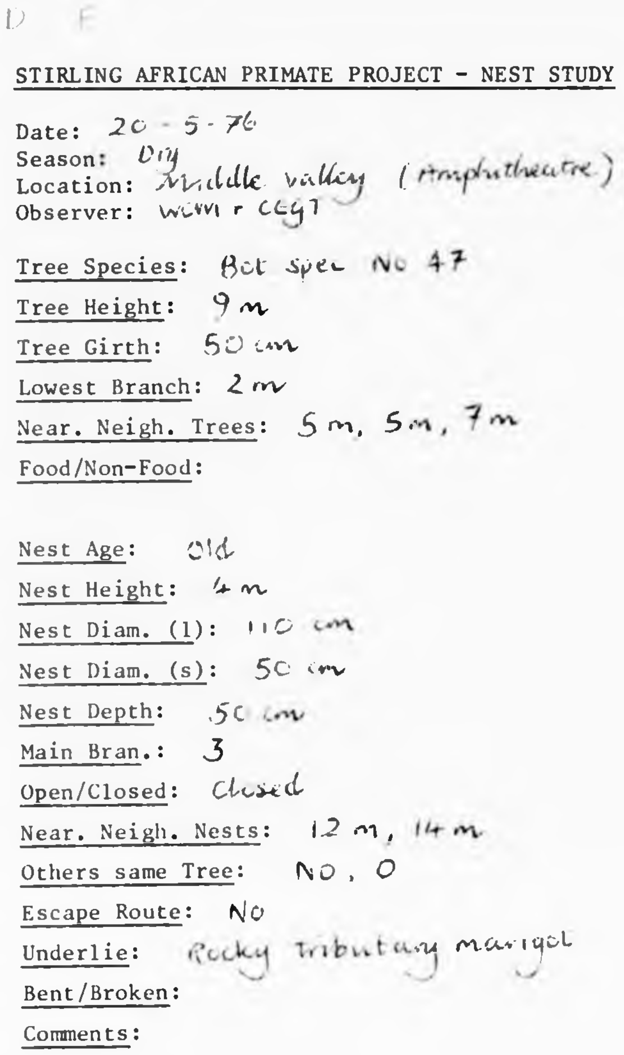
Escape Route: NO

Underlie: Rocky tributary marigol

Bent/Broken:

Comments:

Figure 2. A sample nest card.



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Near. Neigh. Nests: 12 m, 14 m
Others same Tree: NO, 0
Escape Route: NO
Underlie: Rocky tributary marigot
Bent/Broken:
Comments:

Figure 2. A sample nest card.

Stems and leaves of plants were pressed in a standard plant press. Fruits were either pressed in sections, dried whole, or preserved whole in formalin solution. Most specimens remained in good condition, although some were destroyed by fungal growth in the humidity of the wet season. Some specimens were found by Hepper to be infertile and had to be collected a second time. Many specimens still await identification.

4.(iii) Collection of meteorological data.

Initially, only daily maximum and minimum air temperatures, daily rainfall, hourly air temperatures and hourly humidities were recorded in camp. Later, with the exception of rainfall, these measurements were also taken opportunistically at the streambed in the valley. After that, similar data were collected from the plateau. I was interested in the variation between these locations, in case it had an effect on the behaviour of the primates in the area.

All thermometers were placed in well-ventilated positions, 1m from the ground, in the shade. A standard wet-and-dry-bulb thermometer was used to measure hourly air temperatures and humidities. A resettable thermometer was used to measure maxima and minima. Daily measurements were made at 07.00 hours. Hourly measurements were made on the hour until 20.00 hours. A leeway of 5 minutes before or after the hour was permitted for all readings, but an alarm clock was used to aid accurate timing.

Rainfall (in mm.) was measured in a glass rain-guage inside a galvanised iron housing situated in an open area on the plateau.

4.(iv) Sampling the vegetation

The method of transecting to sample vegetation was chosen following the guide of Chapman (1976). A more detailed discussion of the choice appears in Ch. 5. A method was required which assessed the physiognomy of the vegetation rather than one which accurately sampled the frequencies of species: the other priority was that it should be speedy.

The areas sampled by transects were first identified by all researchers as being representative of the type of vegetation chosen. The transects ran following the points of the compass, i.e., north-south or east-west, from starting points chosen for convenience. Fig. 3 shows the beginning of a transect. One north-south transect cut through three types of vegetation. Transects were drawn in different places until totals of 500 metres had been achieved for each type of vegetation. Sampling at more than one location reduced any possible biasses.

The recording of species which occurred on the transect, their heights and girths was performed thus: A 30m. tape measure was laid from the starting point along the compass bearing. All species of which any part touched this line, or the vertical plane above it, were recorded by the distance at which they occurred: their species, height and girth were noted. Height was measured with a tape measure: where this was not possible, heights were estimated: girths were always measured with a tape measure. Multiple trunked trees were recorded as such, and each trunk measured if it was thicker than 10cm; otherwise the collective girth of all the small trunks together was measured. Dead trees or vines, or dead branches of live trees or vines, were ignored: all vegetation less than 2 metres high was ignored. This meant that in general the understorey was not recorded. A single plant that crossed the transect line twice was recorded as occurring only once i.e., the first time that it crossed a part of the line. The number of transects drawn in separate locations for each type of vegetation ranged from 2 to 7.

It can be seen that the method should not be used for measuring the relative frequencies of species within or across samples, especially when the samples are as small as these are. There is a lower probability of a species with a small trunk and canopy occurring on the transect line when compared with the probability of a large trunked or canopied tree occurring on the line: the large tree has a greater area on the horizontal plane and thus more

Figure 3. The start of a transect.

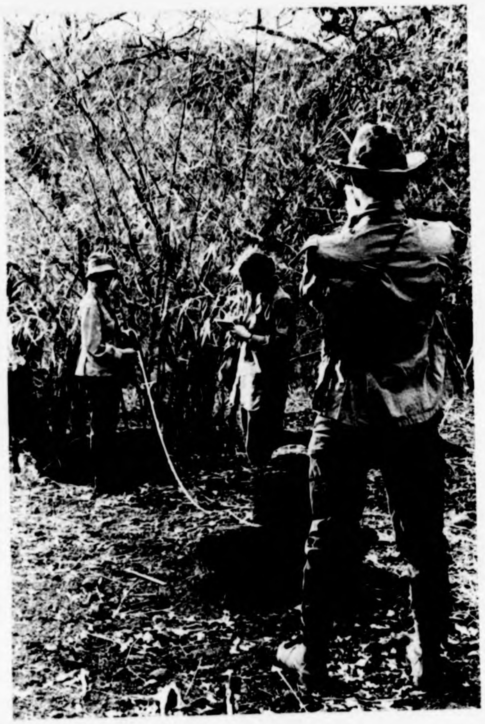
Figure 4. Washing, seiving and examining faeces.

chance of hitting the line, or the space directly above the line. The method can give only an indication of common species within the type of vegetation sampled.

Profile diagrams appear in the Chapter on vegetation as a means of illustrating the physical structure of each type of vegetation; they are taken from samples of the transects. They are constructed by transcribing a length of transect directly onto the diagram: each tree on that sample was drawn to scale height and distance along the line on the profile diagram.

The assessment of the relative amounts of each type of vegetation within the core study area was carried out by placing a grid over a set of aerial photographs; one such photograph appears in Fig. 5, Ch. 6. The grid was made by drawing consecutive squares of side 0.25cm. on acetate paper. This grid was then placed over a matched set of aerial photographs of scale 1cm. = 400m. Thus each cell on the grid represented 1 hectare of land. Each cell was examined under a magnifying glass to determine its type of vegetation. The vegetation was identified by its appearance on the aerial photograph, aided sometimes by memory. Where a cell was split exactly equally between two types, each was recorded as a half-cell: otherwise only the major type was recorded.

Gallery forest appeared solid black on the photograph, since the canopy is closed and no light is reflected off the ground. Woodland was identified by the proportion of tree canopies occupying the hectare: if this was more than 30% of the square, but less than 100% then it was woodland. This is one of the requirements of woodland according to Ellenberg and Mueller-Dombois (1967). The other relevant requirement is that the trees are generally over 5 metres tall: memory was required to decide whether this was the case for each hectare. Unfortunately, grassland and bamboo areas could not be differentiated from each other on the aerial photograph, because both appear uniform grey with scattered trees. Their areas were therefore reckoned together. Plateaux appear blank, usually white or pale grey, and have



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All squares within a circle of radius 10cm. (representing 4km) whose centre is on the summit of Mt. Assirik were recorded by their type of vegetation. These were then transcribed onto the figure which appears in Ch. 5: its scale has been reduced so that 2cm on the figure represents 1km on the ground. From this figure, the relative proportions of types of vegetation occurring within the sample of 50 km^2 were reckoned. It is a time-consuming, but accurate method.

4. (v) Analysis of faeces

In the beginning, the criteria for the collection of faeces were very strict, in order to avoid any possible confusion with the faeces of baboons, which resemble those of chimpanzees when the diets are similar, e.g., when both species are eating large quantities of figs (Ficus spp.). At first, only fresh faeces were collected (i.e. less than 12 hours old and still moist) if they were beneath fresh nests, or were found at a place which chimpanzees were seen to leave. Later, when very fresh faeces were not found regularly, faeces up to 48 hours old were collected, but only if they were beneath nests of the corresponding age. In addition, fresh faeces were taken from areas where chimpanzees had been heard immediately before. After a few months, it was usually possible to discriminate easily between faeces of chimpanzees and baboons, but the later set of criteria were retained as safeguards.

The aim was to sample faeces regularly by the month, with an even spread throughout the month. This was not possible because there were times, especially during the wet season, when we could not find chimpanzees, nor their faeces. As a result, we collected all faeces that we found: some were collected singly and some as part of a large group, and thus cannot be considered as independent samples (see Ch.8 for further discussion of this problem).

Faeces were picked up by hand and put into polythene bags which were sealed until we returned to camp, and were able to analyse them. Faeces were collected as a single sample if they formed a discreet mass. It was more difficult to judge this when they had been dropped from a height, as opposed to being excreted near the ground. When they had fallen from a height, there was usually a central dropping with spattered dung radiating from it. Subtle differences in the hue of the dung helped us to differentiate between two samples if chimpanzees had nested, and subsequently defecated close together. The possibility remains, however, that some collected samples were really two samples lumped together, that some samples were incomplete, or that some were a mixture of separate faecal deposits.

Fresh, moist samples were weighed in camp with a spring balance. Dry faeces more than 24 hours old were not weighed, since evaporation rendered them much lighter. Samples were taken to the stream and placed in a large fine-meshed seive: they were then soaked with water. The contents of the seive were stirred and rinsed repeatedly until the fine faecal matter was washed away, leaving the seeds, fibre, insects etc. (see Fig. 4). Remains were examined and recorded by item with their quantity. Seeds were counted: if they numbered more than 25, then careful estimates of the number were made. An exception was made with fig seeds which were recorded in the same manner as other items for which counting was too time-consuming, e.g., fragments of insects. For these, the judgements of few, common, or abundant were recorded, relative to the size of the faecal sample. Items not able to be identified immediately were preserved in a solution of 10% formalin for future identification.

Chapter 5.

VEGETATION

1. Introduction

In this chapter, certain aspects of the vegetation within a sample of the study areas are described. The aspects chosen are those considered to be particularly relevant to the behaviour of chimpanzees. I shall not attempt to describe the plant ecology *per se*: the purpose of this description of vegetation is to enable the activities of chimpanzees, such as ranging, nesting and feeding, to be related in later chapters to the vegetation within the study area. It is also hoped that the description may be used for the comparison of this habitat with those of chimpanzees elsewhere. The specific aims of this chapter are:

(a) to define different types of vegetation, in terms of their structure and dominant species of woody plants;

(b) to construct a map of the vegetation and to calculate from it the area occupied by each type of vegetation within the sample of the study area;

(c) to describe seasonal differences in vegetation;

(d) to describe other factors affecting the vegetation.

The central core of the study area (see Chapter 3 for definition) was chosen as the sample for the vegetational analysis for two reasons: most importantly, the location (around Mt. Assirik) and size (50 km^2) indicate an area familiar to all observers from daily searches for chimpanzees. In cases where identification of the type of vegetation was difficult to determine from the aerial photograph, first-hand knowledge of an area was used to confirm the type. A circle was chosen simply for ease of analysis: a regular shape is convenient for transposing a grid analysis, and a circle best fitted the most familiar ground.

2. Defining types of vegetation : introduction

The study area contains small areas of vegetation which differ in structure and species. Early in the study, by common sense, we identified 5 types: gallery forest; woodland; bamboo; grassland; plateau. In some places adjacent types merge gradually, elsewhere the change from one to another is abrupt and distinct. Types which often merge gradually are woodland and grassland. Where they abut, there is frequently a transitional area, containing some species typical of woodland and some typical of grassland. By contrast, plateaux and gallery forest are often juxtaposed without a transitional area (see Fig. 1). Whether or not a transitional area occurs depends on the gradation of the soil types and their water-holding capacity. Where no gradation occurs, e.g. where a plateau with poor, thin soil borders a cleft gorge with rich alluvial deposits, the vegetation changes abruptly. Where soil types are similar, and only differ a little in the amount of water they receive from drainage, e.g., in depressions or basins containing clayey soil, the vegetation, in this case bamboo or grassland, will merge together forming a transitional area (see Fig. 2).

As the types differ markedly in their structure and dominant species, it is likely that they are used differentially by chimpanzees. If these differences in usage exist, they may be constant, or they may vary seasonally. Kano (1972) found that in a study of an area of about 3000 km. on the eastern shore of Lake Tanganyika, Pan. t. schweinfurthii mainly frequented riverine forest (structurally equivalent to vegetation termed gallery forest in this study). There was little evidence in the form of food remains, nests, faeces, or direct observation of chimpanzees' using grassland, bamboo bush, swamp vegetation or savanna. In woodland, however, nests were found frequently and 12 observations of chimpanzees were made there. Kano concludes that woodland is used by chimpanzees when travelling from one patch of riverine forest to another and is used only seasonally as a source of food. Unfortunately, no conclusive data were

Figure 1. The juxtaposition of plateau and forest

Figure 2. A gradual transition from grassland, in the foreground, to bamboo, farther away

presented in support of these claims: confirmation will depend on further evidence.

The classification of vegetation into comparable types would enable comparisons of differential usage of vegetation to be made across populations of chimpanzees. The descriptions should include dominant species, since, in some cases, two sites fall within the same vegetational zone, e.g. Gombe and Kasoge in Tanzania. The compositions of species at the two sites are directly comparable, e.g. Saba florida occurs in both areas, but only at Kasoge is it a dominant species and a primary source of food for chimpanzees (Nishida, 1974).

An account of the structure of the vegetation, however, should also be given for broader comparisons. Tree species may be entirely different across habitats, but salient features of structure, such as height of the tree canopy, shade, visibility and density of the vegetation may be matched. Only a description of the physiognomy of the vegetation allows meaningful comparison between two sites which belong to different vegetational zones.

With these two requirements in mind, I attempted to examine and describe the types of vegetation at Mt. Assirik. Only plants over 2 metres high were studied since this included all mature and many immature trees and lianas, but generally excluded the herbaceous layer. This was not examined because it was considered less important to chimpanzees: it is not used for nesting (see Ch. 9), nor for feeding, with the exception of the possible use of some stems as yet unidentified (see Ch. 8). The taller woody vegetation, by contrast, is expected to be most important: chimpanzees spend the night in trees (see Ch. 9) and according to Goodall (1968) they spend 70-80% of their time in trees in the rainy season. Unfortunately Goodall did not state whether this estimation includes night-nesting or not: supporting data were not given. Chimpanzees travel, and sometimes feed and rest, on the ground, but trees are essential in other chimpanzee habitats for shade, refuge and as a source of food, and data from Mt. Assirik confirm this.

Transects were chosen as a form of systematic sampling of the area because the method was the most efficient for our needs (see Ch. 4 for description). We wished to define the types of vegetation on the basis of dominant species and structure. Transects yield information about stratification and density of woody vegetation. They may also be used to calculate individual frequencies of tree species, although the method is less accurate than quadrats for this purpose (see explanation in Ch. 4). They are particularly suitable in areas where zonation occurs (Chapman, 1976, p. 104): this is the case at Mt. Assirik. The method forms the basis for profile diagrams showing the transition from one type of vegetation to another. Most importantly, transects yield useful information in a minimum of time. The main aim of this study of wild chimpanzees was to observe them directly whenever possible, and we were reluctant to spend time on other activities, thus neglecting the continuous tracking of the subjects.

In addition to transecting, the identified types are classified after Ellenberg and Mueller-Dombois (1967). Their system of physiognomic description is designed to accommodate all types of vegetation on a global scale and thus is suitable for a comparative study. At the beginning of each description of a type of vegetation, the appropriate classification according to Ellenberg and Mueller-Dombois (1967) is given.

In naming and describing the types of vegetation at Mt. Assirik, the term 'savanna' has been deliberately avoided for the time being because of its confused usage in the past (Walter, 1971, pp.238-241).

3. Defining types of vegetation: results

Summaries of results from transects appear in Tables 1 and 2. Table 1 presents the mean density, height and girths of trees, bushes, shrubs and lianas in each type of vegetation.

Table 1. The mean density, heights and girths of woody vegetation within each type of vegetation.

Type of vegetation	Total length of transects (m)	Woody vegetation > 2m high		Heights able to be estimated		Measurable girths of single-trunked trees and lianas	
		N	Density of trunks	N	$\overline{X}$	N	$\overline{X}$
Forest	503	231	1: 2.2m	221	10.2m	115	105cm
Woodland	493	138	1: 3.4m	132	6.9m	76	87cm
Bamboo	512	50	1: 10.2m	49	9.3m	30	129cm
Grassland	514	48	1: 10.7m	48	3.5m	24	31cm
Plateau	573	9	1: 63.7m	9	2.6m	-	-
Total	2595	476	-	459	-	245	-
$\overline{X}$	519	95	1: 18m	92	6.5m	61	88cm

Table 2. The number of species, the proportions of bushes, shrubs and multiple-trunked trees and the proportions of bamboo occurring in each type of vegetation.

Type of vegetation	Species of woody vegetation (excl. bamboo)		Bushes, shrubs and multiple trunks		Bamboo clumps	
	N	N in top-ranking 50%	N	%	N	%
Forest	49	7	103	45%	2	0.9%
Woodland	33	5	55	40%	6	4.2%
Bamboo	21	4	19	38%	120	71 %
Grassland	16	3	24	50%	4	7.7%
Plateau	1	1	9	100%	0	-
N	120	20	210	-	132	-
$\bar{X}$	24	4	42	55%	26	17 %

Density refers to the average distance along the transect line between one trunk and the next. The figure was produced by taking the number of metres of transect in each type and dividing by the number of woody plants recorded on it. Not all tree heights were able to be measured by the methods outlined in Chapter 4: some tree-tops were obscured from view: some trees were living, but prostrate, so that measurement of height was not meaningful. Similarly not all girths were measurable, e.g. a strangling fig tree (Ficus umbellata) growing on a cliff face could not be measured unless the cliff could be scaled.

Table 2 shows the diversity of the species in each type of vegetation in two ways: by the number of different species recorded, and by the number of species making up the top-ranking 50% of individuals. This latter reckoning shows whether a few species make up the bulk of the vegetation or if there is a diversity. Table 2 also shows the number of woody plants not having single trunks, i.e., bushes, which have branches occurring at or near ground level; shrubs, in which side shoots are well-developed so that there is no trunk (Usher, 1966); and trees that have more than one trunk emerging from the ground. Finally, Table 2 shows the number of bamboo clumps occurring in each sample of vegetation and the percentage of bamboo accounting for woody vegetation greater than two metres high.

Profile diagrams appear with the detailed descriptions of each type of vegetation (see Ch. 4 for the method). All profile diagrams represent a sample of 100 metres of a transect with the exception of the diagram for gallery forest, which was extended to show a complete cross-section of the valley.

Each type of vegetation will now be described with an elaboration of the results, which appear in Tables 1 and 2.

Gallery forest

This is classified after Ellenberg and Mueller-Dombois (1967) as Tropical (or subtropical) semi-deciduous lowland forest (1.A.3a).

Closed forest is defined as being formed by trees greater than 5m tall, whose crowns interlock (Ellenberg and Mueller-Dombois, 1967). At Mt. Assirik, gallery forest occurs in areas where water is permanent, or long-standing: this is generally in clefts in the plateaux, where erosion has gouged out a gorge. The sections of these valleys that have gallery forest are usually the middle reaches. Here the valleys are narrow, steep-sided, and contain soil that is relatively rich from clayey, alluvial deposits and damp, decaying vegetation. The cover of the canopy is generally continuous, but the stratification is not uniform throughout the forest. Trees are generally tall (see histogram in Fig. 3). The tallest trees, some reaching 40 m, e.g. Ceiba pentandra, are found by the stream-bed: the profile diagram in Figure 4 illustrates this. Presumably trees are tall in this type of vegetation because they have access to more water and richer soil, and because of the narrowness of the cleft, the taller they are, the more light they will receive. All these factors are especially pertinent to trees growing near the stream-bed. Woody lianas, e.g. Saba senegalensis, occur commonly. The floristic cycles of the species, and even of individuals within species, vary, but the forest is mainly evergreen. The herbaceous layer (non-woody vegetation) is sparse or often absent altogether. Most of the woody vegetation (81%) is less than or equal to 15 m in height, but 19% falls into the 16-40 m categories (see Fig. 3). The average height of trees in this type of vegetation is 10.2 m and the average girth of a tree is 105 cm (see Table 1). The woody vegetation is dense, with a plant occurring once every 2.2 m. The vegetation is also more diverse here than in the other types: 7 species account for the top-ranking 50% of woody vegetation. These are termed the dominant species. They are defined as the most common species, ranked by order of frequency (highest first) whose percentages together make up 50% of the sample.

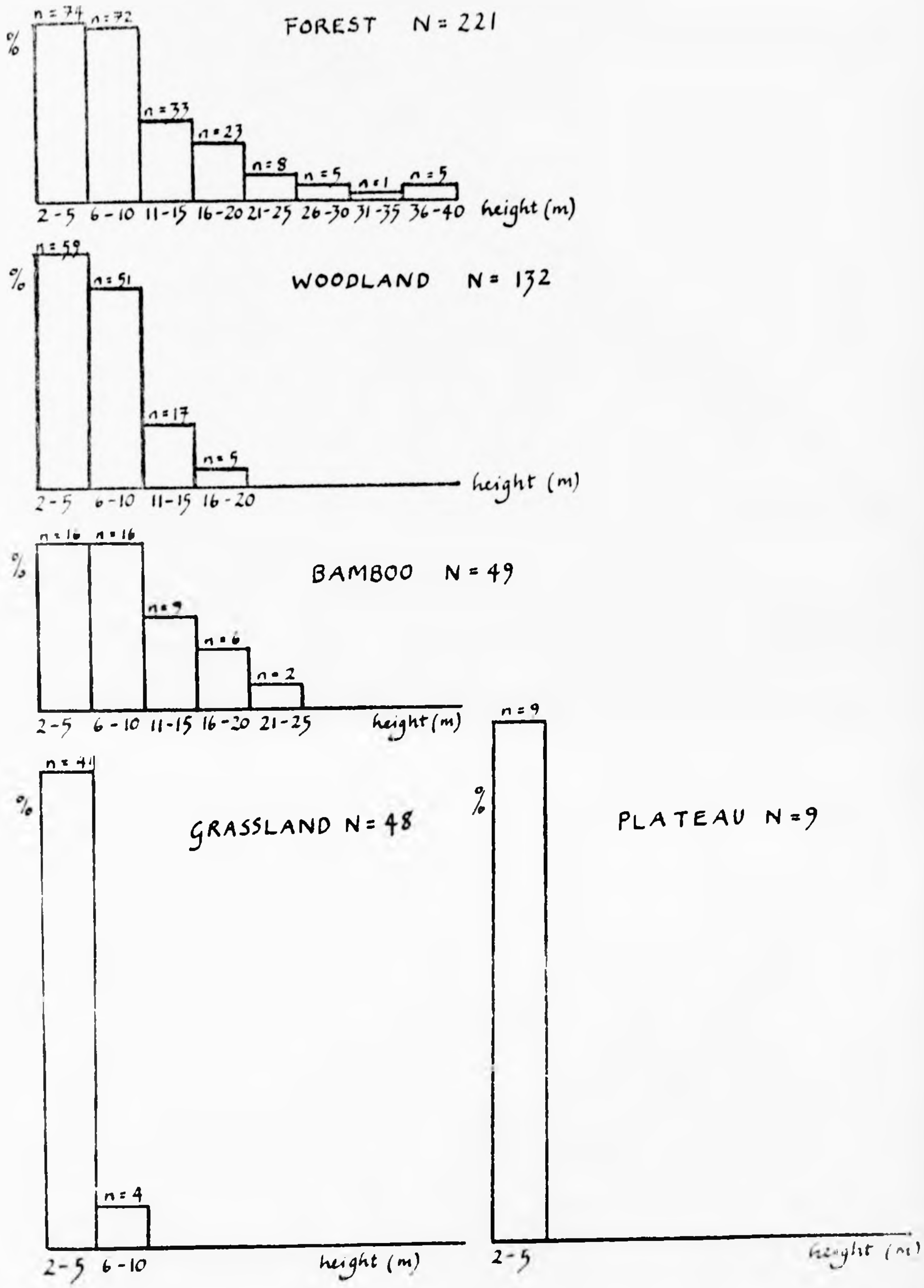
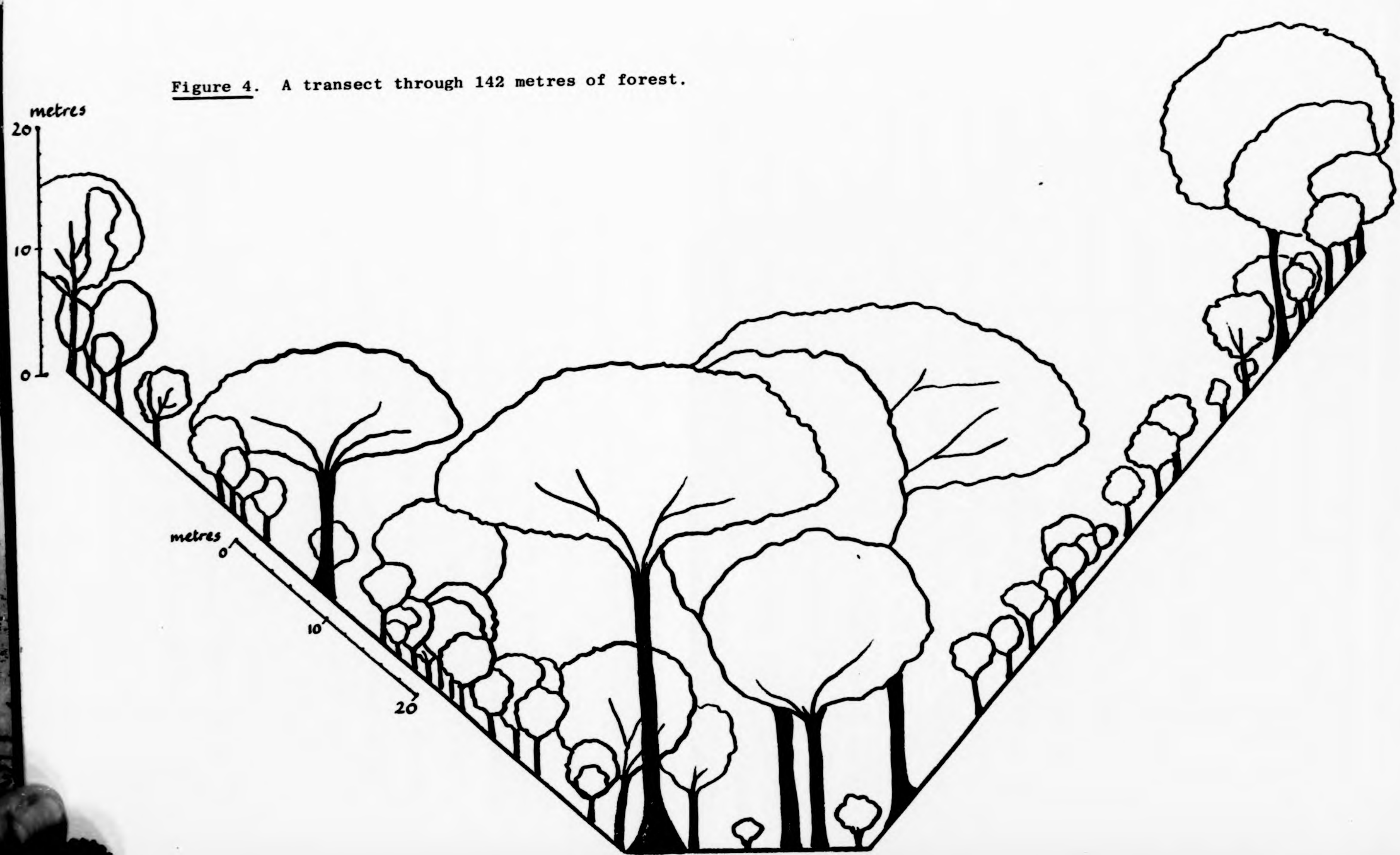


Figure 3. The distribution of heights of woody vegetation within each type of vegetation.

Figure 4. A transect through 142 metres of forest.



The dominant species from all types of vegetation are listed in Table 3.

Woodland

This is classified after Ellenberg and Mueller-Dombois (1967) as Drought-deciduous lowland woodland (II.B.1.a).

Woodland can be distinguished from forest by the fact that in general the crowns of the trees do not touch one another, whereas in forest they do. In woodland, trees are at least 5 metres tall and their canopies cover more than 30% of the ground surface (Ellenberg and Mueller-Dombois, 1967). At Mt. Assirik it is found on the gentler slopes of valleys and hillsides. It occurs where erosion has taken away the surface layer of soil, leaving the poorer sandstones (Adam, 1971). The soil is well-drained, retaining little moisture near the surface after rain. The cover of the canopy is not continuous: the density of woody vegetation was found to be on average one plant every 3.4 metres. The trees are not as tall as they are in the forest: 83% of trees were 10 m or less in height: no trees taller than 20 m appeared in the sample (see Fig. 3). The stratification varies less than in forest but there is a slight tendency for trees to be taller nearer a streambed (see the profile diagram in Fig. 5). The vegetation is deciduous, with trees shedding their leaves in the dry season. There is a sparse herbaceous layer, consisting mainly of grasses, which may grow to a height of 2 metres. Some bamboo occurs occasionally (see Fig. 5 and Table 2). Woodland is less diverse in its species than forest: 5 species account for the top-ranking 50% of woody vegetation. The average height of this vegetation is 6.9 m and mean girth of woody plants is 87 cm.

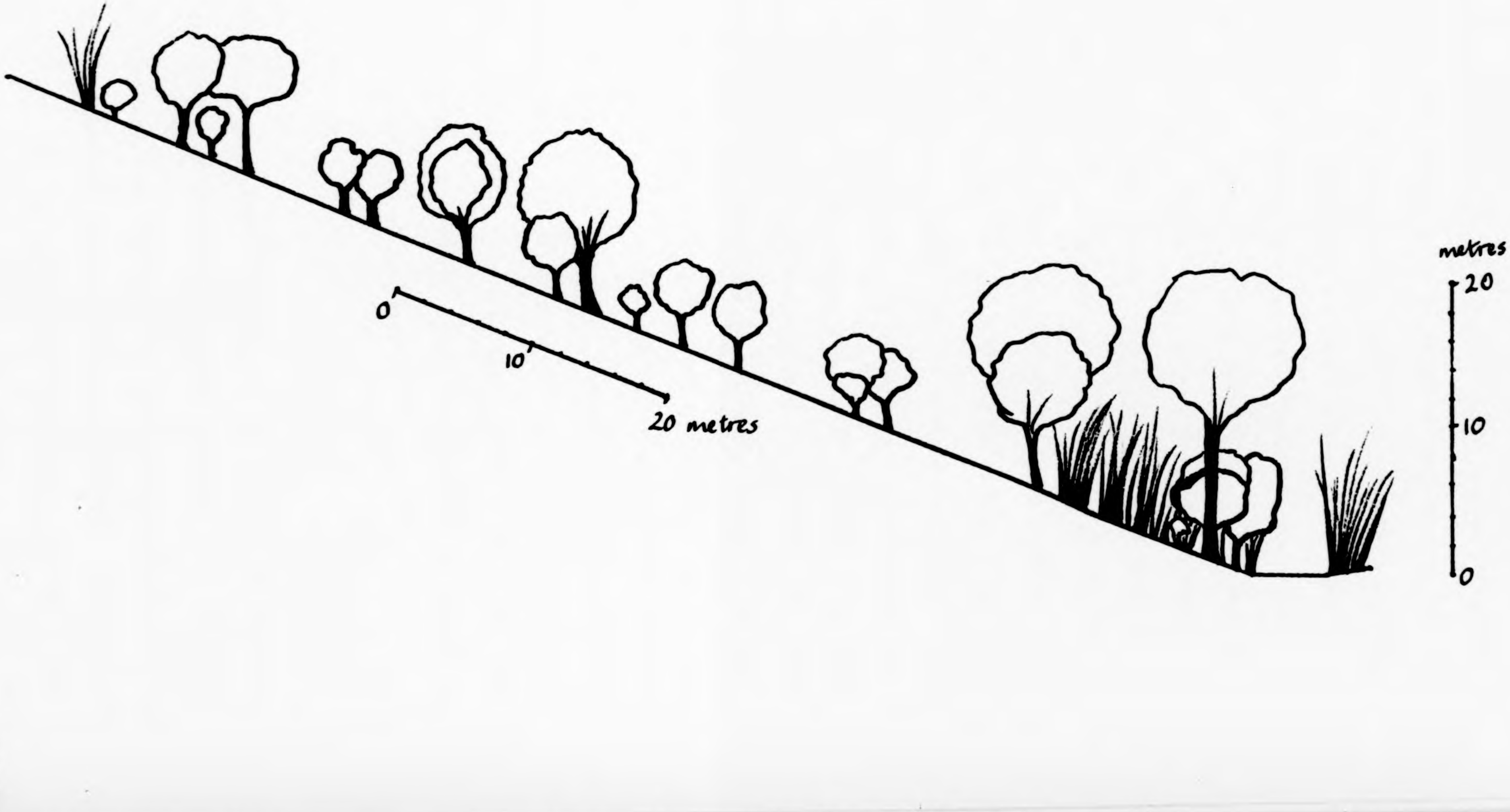
Bamboo

This is classified after Ellenberg and Mueller-Dombois (1967) as Flat-leaved tree savanna with isolated palms and deciduous trees (V.A.1.b (2) and (3)).

Table 3. A list of dominant species (i.e. those in top-ranking 50%) in each type of vegetation, with their mean heights.

Type of vegetation		Species	Mean height
FOREST	1.	Not yet identified (A)	5.6 m
	2.	*Saba senegalensis*	8.7 m
	3.	*Combretum tomentosum*	8.2 m
	4.	Not yet identified (B)	8.5 m
	5.	*Oncoba spinosa*	6.1 m
		Ficus umbellata	16.2 m
		Diospyros mespiliformis	7.1 m
WOODLAND	1.	*Hexolobus monopetalus*	4.8 m
	2.	*Pterocarpus erinaceus*	9.5 m
	3.	*Afzelia africana*	10.9 m
	4.	Not yet identified (C)	4.4 m
	5.	*Vitex madiensis*	2.8 m
BAMBOO	1.	Not yet identified (C)	3.9 m
	2.	*Pterocarpus erinaceus*	10.6 m
	3.	*Acacia macrostachya*	16.8 m
	4.	*Piliostigma thonningii*	6.7 m
	5.	*Diospyros mespiliformis*	7.0 m
GRASSLAND	1.	*Crossopteryx febrifuga*	3.6 m
		Not yet identified (C)	3.1 m
		Not yet identified (D)	3.0 m
	2.	*Annona senegalensis*	2.3 m
		Not yet identified (E)	8.5 m
		Not yet identified (F)	5.5 m
PLATEAU	1.	*Combretum collineum*	2.6 m

Figure 5. A transect through 100 metres of woodland.



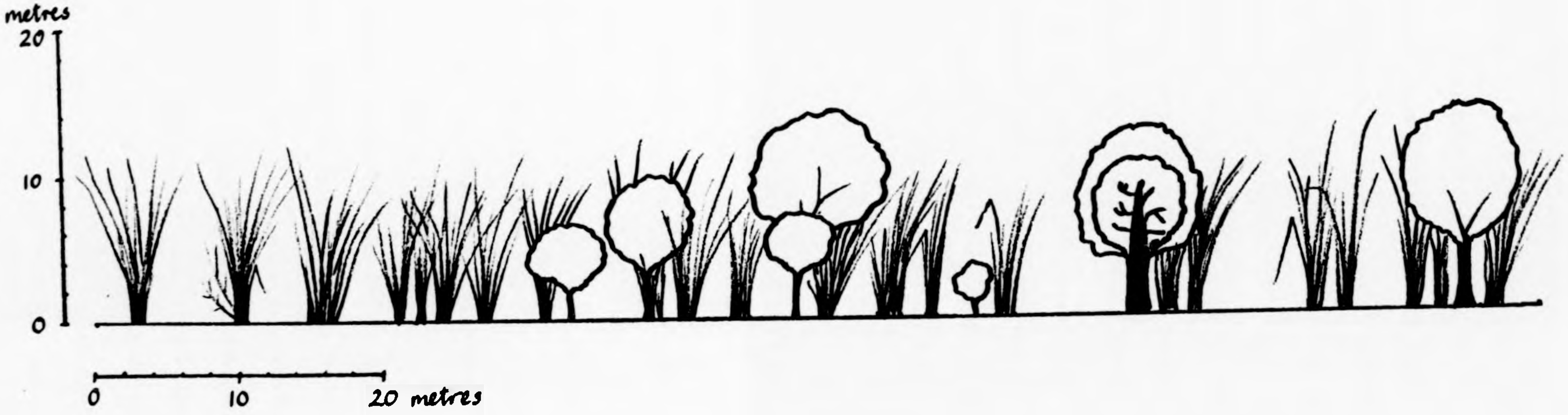
Bamboo (Oxytenanthera abyssinica) occurs in various places throughout the study area but it forms dense cover in areas of clayey soil: in large depressions and in the lower, open sections of valleys. The areas are water-logged in the wet season and dry for the rest of the year. Where bamboo appears in profusion, isolated tall trees are scattered regularly throughout it (see profile diagram in Fig. 6). These species are often recognised savanna species, e.g., Acacia sp., or big trees which can store water, e.g., the baobab (Adansonia digitata) and a palm (Borassus flabellifer). Clumps of bamboo were on average 127 cm.wide and occurred every 4.3 metres: their thick shade seems to prevent a herbaceous layer from forming below. Most bamboo grows to a height of about 9 m, and the few trees are scattered, on average one every 10.2 m. They are large, with an average height of 9.3 metres and a girth of 129 cm. Trees are comparatively scarce here, presumably because of the lack of water available: bamboo, with its shorter root system, can take advantage of the surface water in the wet season and needs little in the dry season: those trees which grow here must manage with little water, or else store it. Trees are tall (see Figs. 3 and 6) in order to reach the light otherwise obscured by the stands of bamboo. Bamboo itself was easily the most dominant form of vegetation, accounting for 70.6% of recorded plants. There are few vines and lianas. Even without the bamboo, the woody vegetation is still less diverse than either woodland or forest: 4 species account for the top-ranking 50% of the sample.

Grassland

This is classified after Ellenberg and Mueller-Dombois (1967) as Narrow-leaved savanna with isolated deciduous trees (V.A.2.a(2)).

Grassland is distinguished from woodland with some grass growing in it, by the fact that in grassland the canopies of trees cover less than 30% of the ground. Grassland occurs in the same kind of terrain as the bamboo, i.e., clayey soil in poorly drained depressions. It differs structurally from

Figure 6. A transect through 100 metres of bamboo.



bamboo in that although trees occur at roughly the same density, one every 10.7 metres (see Table 1) they are not so tall (see Figs. 3 and 7). The mean height of the woody vegetation in grassland is only 3.5 metres. This presumably stems from less available water, a factor which probably explains why grasses rather than bamboo grow in these areas: trees do not have to reach the same heights as in bamboo in order to reach the light. The grass cover is continuous and generally grows to a height of 1.5-2 metres. It yellows during the dry season and usually burns off. The species of woody plants occurring in grassland are not diverse: only 3 species account for the first-ranking 50% of the sample. One of these, a species of Combretum, is also a dominant species in the bamboo and woodland areas. The low, scattered woody plants in grassland comprise a high proportion (50%) of bushes, shrubs and multiple-trunked trees (see Table 1).

Plateau

This is classified after Ellenberg and Mueller-Dombois (1967) as Narrow-leaved savanna with isolated deciduous shrubs (V.A.2.b. (2)).

The term, plateau, refers not only to the terrain but to the uniform type of vegetation which grows on it at Mt. Assirik. The plateaux are solid sheets of bauxite or laterite with a thin, mixed layer of poor, sedimentary soils. Sometimes even this is absent. Plateaux can support only sparse vegetation: this consists mainly of bushes of Combretum collineum and short grasses, less than a metre high, that grow in the wet season. Often these bushes grow out of active or abandoned termite mounds (see Fig. 8). The mounds provide deeper, well-drained, rather than richer, soil (Walter, 1971). The bushes also grow round the edges of the plateaux where cracks have appeared in the laterite cap. During the rainy season the abundant rain allows grass to grow, despite the fact that water quickly runs off the plateau and that any pools of water are soon dried by the heat. When the rain ceases at the end of the wet season, moisture evaporates fast on these open areas, and the grasses soon die. In our transect samples,

Figure 7. A transect through 100 metres of grassland.

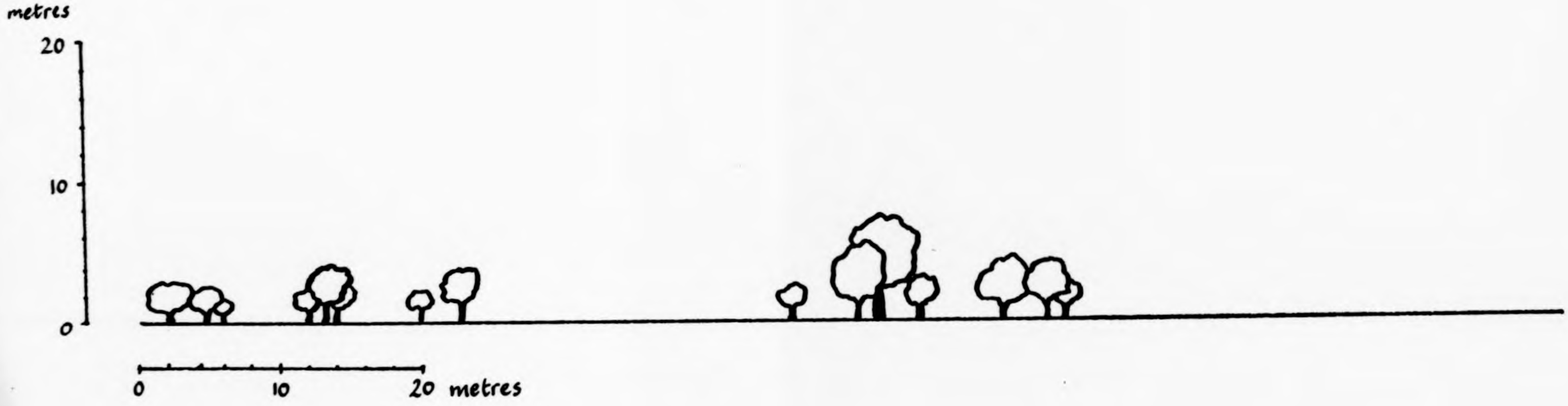
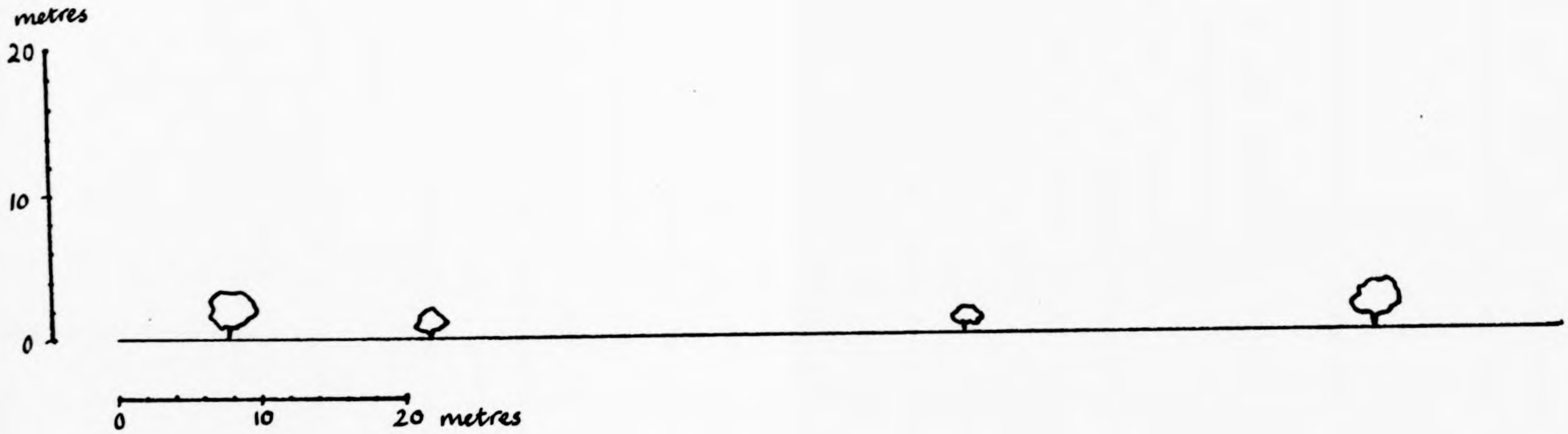


Figure 8. A combretum bush growing out of a termite mound.

Figure 9. A transect across 100 metres of plateau.



Combretum collineum was the only woody plant occurring on the plateaux. The bushes were on average 2.6 metres high and 63.6 metres apart (see Fig. 3, and the profile diagram in Figure 9).

4. A map of the vegetation and quantifying types of vegetation: introduction

A map of the vegetation of a study area enables searching routes to be described in terms of the types of vegetation encountered. Traces of chimpanzees can then be recorded with the type of vegetation in which they were found. Among studies of wild chimpanzees, a quantification of types of vegetation has been carried out before only by Kano (1972). He examined vegetation in breadth during a survey of the eastern shore of Lake Tanganyika, Tanzania. His method involved a kind of transecting along survey routes of varying length, which he made on foot. Where the survey route entered and left a type of vegetation, the point was marked and then the percentages of these different types were computed. Only for riverine and mountain forests could more accurate estimates of the surface area occupied by each type be made from aerial photographs, although Kano provided no account of the method used. He claimed that other types of vegetation could not be identified from the aerial photograph. Presumably this was because the other types were mainly classes of woodland, and although the structure could be identified on the photographs, dominant species could not. It is a pity that no other ecological study of chimpanzees has quantified types of vegetation, particularly at the long-term sites such as Gombe or Kasoge, Tanzania.

The method used to map and to quantify the types of vegetation at Mt. Assirik is described in Chapter 4. The sample area is a circle about Mt. Assirik with an area of 50 km^2.

5. A map of the vegetation: results

A map of the types of vegetation within the core study area can be seen in Figure 10. The resulting proportions of these types are shown, in percentages and in km^2, on a pie-chart in Figure 11.

Since grassland and bamboo areas could not be quantified separately by the method used (see explanation in Ch. 4) they are pooled in the results. As an informal estimate, bamboo occupies about 5% of the sample, and grassland about 27%.

The type of vegetation covering the most surface area is woodland with 37% or 189 hectares, but the areas covered by grassland and bamboo (32%, 164 hectares) and by the plateaux (28% and 143 hectares) are of similar proportions. It is surprising to see that forest occupies only 3%, that is 14 hectares, of the study area. The total of hectares is 510, rather than 500, which would be the case if the circle of the sample were exactly 50 km^2 : the explanation for this is that the circle's area is more precisely 503.52 hectares ($r=4$, $\pi r^2 = 50.352$ km^2). In reckoning the types of vegetation from the grid over the aerial photograph, cells on the perimeter were included even if part of the cell fell outside the circle. These are both factors in the slightly higher total surface areas, It may be that both forest and woodland areas are slightly under-estimated: this is because both these types of vegetation frequently occur on slopes of varying angles. Viewed on a two-dimensional photograph, the surface area will be underestimated: the amount of the error was estimated by sampling the angles of slopes 20 times in each type of habitat..Mean angles were calculated for each type of vegetation and the natural secants of these were multiplied by the surface area found on the aerial photograph. The results give the approximate underestimation for each type of vegetation and are shown in Table 4. In no case were whole percentages altered.

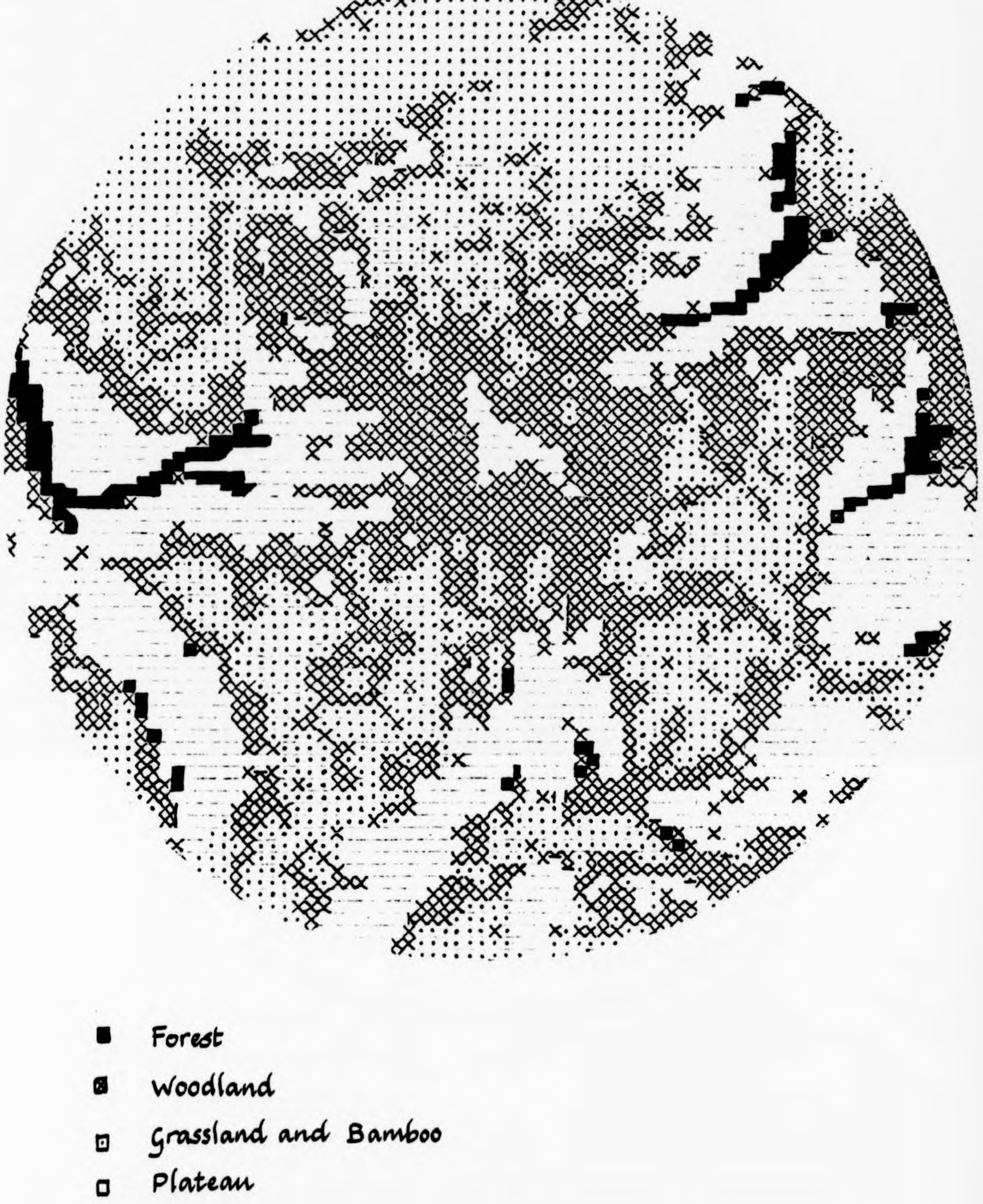


Figure 10. The map of vegetation in the core study area.

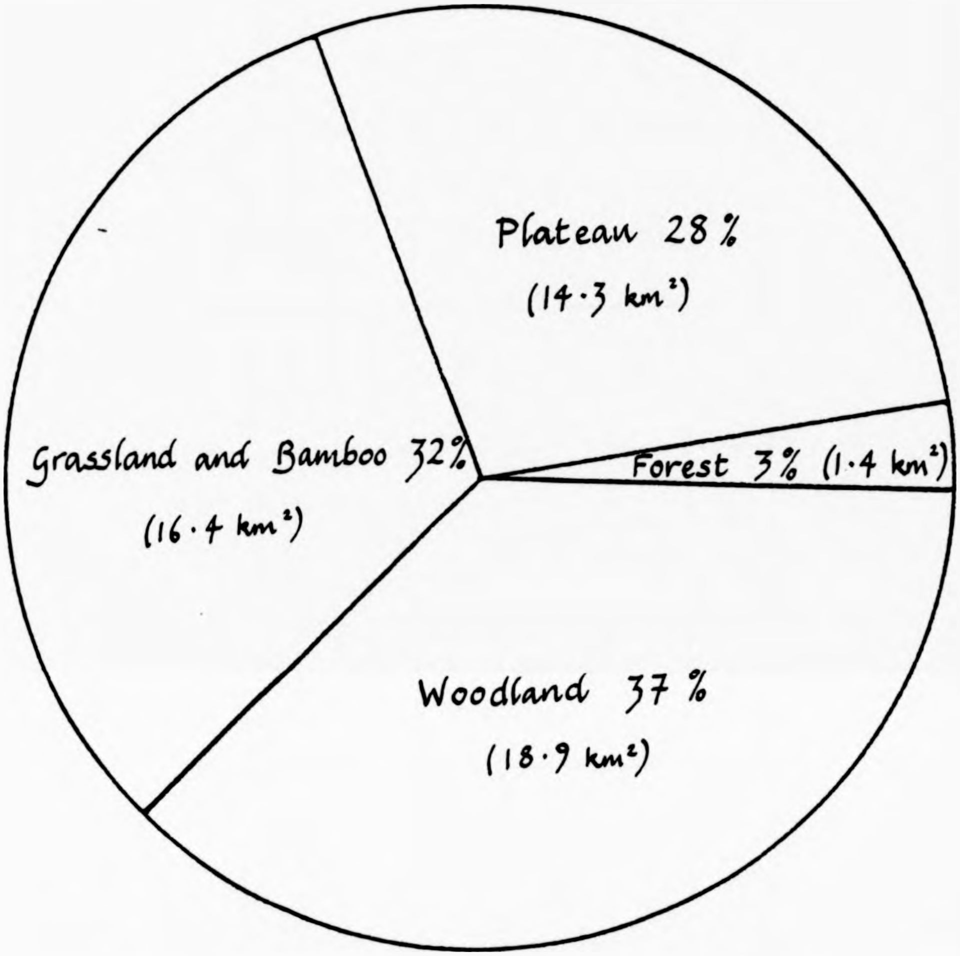


Figure 11. A pie chart showing the relative proportions of types of vegetation in the core study area.

Table 4. The adjustment of surface areas of vegetation measured from aerial photographs: the original surface areas are multiplied by the natural secants of their mean angles.

Type of vegetation	Area from aerial photo (hectares)	Mean angle of slope	Range of slopes	Natural secant	Adjusted area (hectares)	% area
Forest	14	23^o	$3 - 90^o$	1.0864	15.2	3%
Woodland	189	12^o	$2 - 24^o$	1.0223	193.2	37%
Bamboo & Grassland	164	5^o	$0 - 15^o$	1.0038	164.6	32%
Plateau	143	2^o	$0 - 8^o$	1.0006	143.1	28%
TOTAL	510	16^o	$0 - 90^o$	-	516.1	100%

6. Seasonal changes in vegetation: introduction

Among primates there are many examples of seasonal differences in ranging. Many of these are due to seasonal differences in vegetation, which result in an altered distribution of food, e.g., *Papio ursinus*, *Papio anubis* (DeVore and Hall, 1965), and *Theropithecus gelada* (Crook and Aldrich-Blake, 1968). Some changes in ranging are due to the altered distribution of water, e.g., rhesus monkeys, *Macaca mulatta* (Lindburg, 1977). In more open habitats with large seasonal differences in climate and subsequent changes in vegetation, differences in behaviour would be expected: Mt. Assirik is such a place.

Apart from the expected changes in the distributions of food and water at Mt. Assirik, in the areas of primarily deciduous vegetation, one expects to find higher air temperatures, increased visibility, greater risk of burning (see next section) and more reduced foliage for feeding and nesting material, than in the areas in which there is little shedding of leaves. All the conditions of the deciduous vegetation mentioned above suggest the hypothesis that these areas are less hospitable for chimpanzees in the dry season than in the wet, and that they will prefer mainly evergreen areas in the dry season regardless of the amount of food available in each type of vegetation. If this were true, it would be in contrast to the other chimpanzee habitats (Sugiyama, 1968; Nishida, 1974; Wrangham, 1975) where changes in ranging and dispersion are thought to relate only to the availability of food.

7. Seasonal changes in vegetation: description

Forested areas are least affected by the seasons. Although in the dry season the foliage is reduced, because at this time most trees shed leaves and then show new growth, the change of leaves occurs at different times for different species and for individuals within species. Thus the canopy is reduced, but cover remains continuous. Since there is little or no herbaceous layer in the gallery forest, the undergrowth does not alter appreciably (see Fig. 12).

Woodland is transformed by the seasons (see Fig. 13). Most trees are deciduous and begin to shed their leaves in the second month of the dry season. They remain leafless for a further four months and then about a month before the rains begin, they start to show flushing leaves. By the onset of the rainy season they have a thick growth of new leaves, and this growth continues throughout the rainy season. The grasses beneath the trees, e.g., Pennisetum hordeoides, Panicum phragmitoides, also begin to grow just before the wet season and continue to grow throughout the rains. With the onset of the dry season the grass yellows as the upper parts of the plant die. Fire often destroys these parts so that only the rhizomes remain, waiting to put out new growth at the beginning of the following wet season.

In areas of bamboo, the trees are deciduous and shed their leaves in the dry season in the same manner as those in woodland. At the same time, the leaves of the bamboo turn yellow and about three-quarters of them fall to the ground (see Fig. 14). As with the species of grasses in the woodland, the bamboo puts out new growth just before the rainy season.

Grassland follows a similar pattern to the bamboo, with the trees shedding their leaves in the dry season and the grass dying at the same time (see Fig. 15). One difference is the effect of fire which sweeps through grassland in the dry season but has little effect on the fire-resistant bamboo.

Plateaux have quite different appearances in the two seasons (see Fig. 16). In the wet season, they are covered with short grasses such as Cyathula pobeguinii, Loudetiopsis tristachyoides, or Ctenium villosum, which grow to a height of about a metre, and the Combretum bushes are well-leafed. At the beginning of the dry season, the grasses turn golden yellow and the plateaux resemble vast cornfields. As the dry season progresses, the grasses collapse with the trampling of animals and the effects of wind.

Figure 12. Forest in the wet season (above) and in the dry season (below).

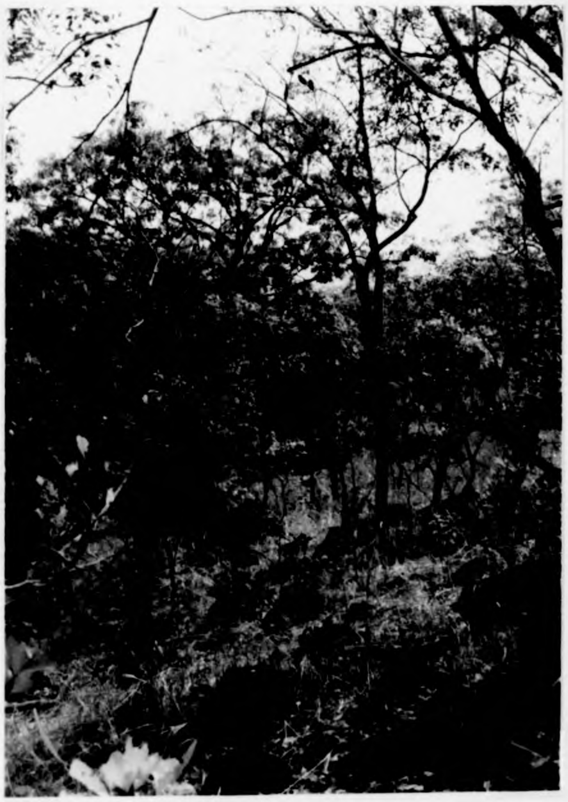


Figure 13. Woodland in the wet season (above) and in the dry season (below).

Figure 14. Bamboo in the wet season (above) and in the dry season (below).

Figure 15. Grassland in the wet season (above) and in the dry season (below).

<u>Figure 16</u>. Plateau in the wet season (above) and in the dry season (below).

Most plateaux are burnt by fires in the dry season (see Fig. 17). These consume the grasses and scorch the leaves of the Combretum bushes, leaving the plateaux looking like the surface of the moon, bare and open.

8. Other factors affecting the vegetation

8 (i) Fire

It is the policy of the Parc National du Niokolo-Koba to start fires in certain areas to burn off the grass. The purposes for this are diverse: to open up the tracks for tourists; to clear vegetation enabling a better view of the wildlife for tourists; to make firebreaks in order to prevent more extensive burning by other agents; to encourage better growth by clearing dead vegetation; and to add more nutrition to the soil and thus to the fodder of ungulates (Dupuy, 1971, p.236). The fires tend to spread through the park and are not as localised as planned. Before the creation of the park it is possible that hunters used fire to drive game in a desired direction: this method may still be used by poachers. Fires may also be started by natural causes, as a result of lightning (Phillips, 1974). It seems that fire may well be a long-established factor in the Mt. Assirik ecosystem.

Some of the species at Mt. Assirik seem to be resistant to fire and put out new growth after having their leaves scorched. A clear example is the Combretum of the plateaux which can lose all its leaves, have its bark charred and blackened, and then put out new leaves within a fortnight.

The timing of the fire appears to be critical. The drier the vegetation, the more fierce and damaging the fire. Fires at the beginning of the dry season burn only the driest sections of the grass and rarely reach such intensity as to damage trees seriously: late dry season fires rage throughout the undergrowth, burning whole trees, and entering the areas of forest where they burn the dessicated leaf litter. Figure 18 shows an early dry season fire on a plateau.

Figure 17. A comparison of burnt plateau (on the left) with unburnt plateau (on the right).

Figure 18. Fire on the plateau.

8. (ii) Human effects

As mentioned in Chapter 3, there were human settlements in the core study area some 20-50 years ago, but no relic domestic trees have been discovered. Just outside the core study area, there are hut remains in the form of circles of stones and at that site there are two mango trees (Mangifera indica).

Present-day human influence is also negligible. Poachers may sometimes start fires, otherwise they damage little, cutting single saplings for bamboo stems for ladders to reach bees' nests, or for their tripodal hides.

For our own surveys we used existing animal paths. Two of these were widened and the vertical space above them cleared. They ran along the edges of Lion Valley for a distance of about 1 km. each. The clearance involved removing large stones from underfoot and trimming protruding branches up to a height of about 2 metres.

Transecting involved no damage at all.

8 (iii) Animal effects

Elephants were seen to be destructive in the study area: they broke branches, stripped bark extensively and uprooted trees of up to 5 metres in height during the course of their feeding. They were only occasional visitors to the study area, however, and did not usually stay for more than a week at a time.

Chimpanzees themselves destroyed branches when feeding, playing and nesting, by bending and breaking them. They also stripped bark from trees. No trees were seen that had been killed as a result of this behaviour.

Termites generally consumed dead wood on the ground and dead branches of live trees, but seldom killed trees by this activity. They may even encourage vegetational growth by providing mounds of deep earth which allow plants to grow on surfaces that could not otherwise support them, e.g., mounds of Cubitermes niokoloensis supporting bushes of Combretum collineum on the plateaux. This particular association was noticeable and so, out of curiosity, a series of samples were taken. Five squares with 25 m sides were randomly chosen on five different plateaux. Within these squares, the number of Combretum bushes, the number of termite mounds, and the number of these two occurring together were counted. A sign test revealed that the number of termite mounds occurring alone and the number of Combretum bushes occurring alone were both significantly fewer than the number of these two occurring together (N=5, x=0, p= 0.03, one-tailed tests). Thus there is a tendency for them to occur together: this seems likely to be due to the advantage for the Combretum bush to grow on the mound, rather than termites being attracted to the bushes, since the bushes appeared to be untouched by the termites in those mounds that were active (N=55 or 58% of mounds).

9. Discussion

In this description of vegetation, three issues are raised:

(1) To what extent is the vegetation at Mt. Assirik natural?

(2) How does it compare with other places where chimpanzees are found?

(3) What influence might this vegetation have on the wild chimpanzee?

The fourth part of the description of the vegetation showed that it is little distrubed, with the exception of fire. Fire most seriously affects the areas of plateau, grassland and woodland. The important question raised is whether the vegetation at Mt. Assirik would be the same without annual burning.

Walter (1971) pointed out that annual burning, intentional or accidental, has changed many natural woodland areas to grassland, or 'secondary savannah'. Natural savanna occurs with a specific combination of climate and type of soil. Undisturbed areas give rise to different types of vegetation according to the soil's richness and water-retaining properties. Forest occurs where the soil is both rich and moist: woodland occurs where the soil is less rich and coarse-textured. On such soil, woody plants still dominate over grasses because their extensive root systems can reach down through the rough ground to obtain sufficient water. The grassland of Mt. Assirik, which according to Walter (1971) is a form of savanna, occurs naturally where the soil is finer and has a higher capacity to hold water close to the surface. Grasses dominate over woody vegetation because they can absorb much water in the growing (wet) season and need practically no water in their dormant period, i.e., in the dry season when surface water has evaporated. If rainfall is sufficiently high, grasses will not take up all water, and scattered woody plants, often shrubs, can make use of the residual water.

The grassland at Mt. Assirik thus appears to comply with these conditions and to be the natural product of the climate, and the type of soil on which it grows.

It would also seem to be the case that the plateaux could not support more trees, even without the annual burning, since trees cannot compete with grasses on that type of soil; so it is with bamboo also.

All types of vegetation at Mt. Assirik seem to be structurally, naturally adapted to their conditions of soil and water.

The only difference between the vegetation as it is now,and as it would be without burning, is likely to be in the species that occur at Mt. Assirik. It is possible that some species that are not resistant to the effects of fire have disappeared: the structure of the vegetation, however, seems to be entirely natural.

A quantative comparison of the vegetation at sites where chimpanzees have been studied is hindered by the lack of available data from elsewhere, but it appears that Mt. Assirik has the most sparse vegetation of all. Fortunately, the habitat that seems to be most similar is the one for which quantitative data are available: this is the area on the eastern shore of Lake Tanganyika, studied by Kano (1972). The estimates made by him were from survey routes (as explained in the introduction to the second section of this chapter) and were approximations. The exception was with the forested areas, which were reckoned from aerial photographs. Moreover, the distance through the chimpanzee distribution that he used for the survey was 679.5 km. This must have passed through several separate community ranges that were not necessarily contiguous. Some of the ranges will have different proportions of the types of vegetation than those presented in Table 5. This table compares the proportions found by Kano with those at Mt. Assirik.

As the table shows, the woody vegetaion at Mt. Assirik is more sparse than that found by Kano. Riverine forest (structurally equivalent to the gallery forest at Mt. Assirik) formed 5% in Tanzania, but only 3% at Mt. Assirik. Woodland at Mt. Assirik is also proportionally smaller than in Tanzania, 37% versus 58%. Both these types of vegetation have been considered important for chimpanzees, with forest being most important. Kano did find one area of chimpanzee distribution with even less forest than Mt. Assirik, i.e., the Ugalla region, but there woodland occupies 91.3% of the land. Thus the Ugalla region has a much greater proportion of woody vegetation than has Mt. Assirik. This is also the case with four other areas found by Kano to have less than 5% forest; all are compensated by larger proportions of woodland. This appears to be the case at Gombe as well, from the diagram given by Wrangham (1977, p.505), although total surface areas are not presented. Thus all the habitats thought of as the savanna habitats for chimpanzees are richer in woody vegetation than Mt. Assirik.

The other sites where chimpanzees have been studied for extended periods are forested areas: the Budongo Forest is a tropical rain forest, containing five distinct types of forest within it (Reynolds and Reynolds, 1965). Mt. Okoro-Biko and Mt. Alen in Rio Muni also lie within tropical

Table 5. A comparison of proportional types of vegetation. (Percentages from Kano (1972, p.70) are adjusted to include forest.)

Type of vegetation	Eastern shore, Lake Tanganyika (Kano, 1972)	Mt. Assirik	
FOREST	5%	3%	
WOODLAND	58%	37%	
BAMBOO	9%	est. 5%	32%
SAVANNA	14%	est. 27%	
GRASSLAND	9%		
SWAMP	5%	-	
PLATEAU	-	28%	

rain forest (Jones and Sabater Pi, 1971).

Perhaps such a breakdown is a little simplistic: other factors may be important in estimating usable vegetation for chimpanzees, e.g., the diversity of species in each type of vegetation. Even in this respect, however, Mt. Assirik is comparatively poorly off. In Gabon, Hladik (1977) listed 15 species accounting for the top-ranking 50% of trees. At Gombe, the data for the range of chimpanzees have not been collected, but in the riverine forest used by red colobus monkeys (Colobus badius tephrosceles), 9 species account for the first 50% (Clutton-Brock, 1977). In the gallery forest at Mt. Assirik 7 species constitute the top-ranking 50% of trees.

If the chimpanzees at Mt. Assirik are as deprived, in terms of the vegetation, as they seem to be, interesting speculation arises concerning the way in which this might affect their behaviour.

First: it has been indicated from elsewhere that in areas which are dry, i.e., with seasonal rainfall less than or equal to about 1000 mm., and which have comparatively sparse vegetation, the density of chimpanzees is low. At 7 sites on the eastern shore of Lake Tanganyika, Kano (1972) found a mean density of 0.21 chimpanzees/km^2. These areas are on the fringe of the distribution of Pan troglodytes, as is Mt. Assirik. These low densities are associated with large home ranges (Kano, 1972). The relationship between the dry, open vegetation, and the low density with large home range is difficult to confirm: to calculate density and home range one needs to know the number of individuals in the population under study and the movements of each one over the course of at least a year (see Ch. 6). The population should not be provisioned, since this could alter the pattern of ranging. In Kano's study, the chimpanzees were not provisioned, and the emphasis of the study was on the environment. In 10 months there was little opportunity to learn much of the 1,700-2,000 chimpanzees thought to exist in the study area. No long-term, detailed study of chimpanzees, without provisioning, has been undertaken in a dry, open habitat. This study hopes to elucidate the suggested relationship between open vegetation, density of chimpanzees and the size of home range in a dry habitat in the following chapter.

Second: it appears that the percentage of forest at Mt. Assirik is minimal. This has been found to coincide with large percentages of woodland in other chimpanzee habitats. Mt. Assirik has a comparatively small percentage of woodland: the rest of the vegetation is of a kind which is scarcely used elsewhere. In order to adapt to the vegetation at Mt. Assirik it is hypothesized that chimpanzees must either use these 'undesirable' areas - bamboo, grassland and plateau; or else range over a large surface area in order to reach sufficient areas of forest and woodland for their needs. They may do both.

Chapter 6. RANGING, GROUP SIZE AND DENSITY

Introduction

There were three important reasons why the factors of ranging, group size and density should be examined in the population at Mt. Assirik. Firstly, recent interest in systematic, comparative primate ecology, e.g. Clutton-Brock, 1977; Milton and May, 1976, requires comprehensive knowledge of the ecology of chimpanzees in different habitats. This population exists on the fringe of the distribution of Pan troglodytes in the most open habitat, in terms of woody vegetation, that has been recorded for the species (see Ch. 5). Information on their ranging, group size and density are necessary for inclusion with other, more hospitable chimpanzee habitats, for a true assessment of the adaptibility of the species.

Secondly, no study of the subspecies Pan t. verus has lasted long enough to be able to measure these factors over the course of a year. A long-term study is necessary to examine seasonal changes in behaviour. Examples of these have been seen already in other populations, e.g. a shift in range in the Mahali Mountains (Nishida and Kawanaka, 1972); a change in the size of groups in the Budongo Forest (Reynolds and Reynolds, 1965; Sugiyama, 1972).

Thirdly, it is now accepted that early hominids evolved in the savanna regions of Africa. While baboons (Papio sp.) are the most successful ground-dwelling primates living in savanna regions today, and aspects of their behaviour must suggest adaptations made by early man, wild chimpanzees have a unique role to play in enlightening the subject. Chimpanzees make and use tools (Beck, 1975); they have the ability to use language and therefore the cognitive means for advanced social communication (Premack, 1976). They can be studied now on a scale of varying environments. By looking at critical differences in their ranging and social organisation in these different habitats, we may glean clues as to why a savanna environment was advantageous to man's evolution.

This chapter attempts to answer four questions:

1) Which types of habitat do the chimpanzees use, and is there a seasonal difference in this usage?
2) How far do chimpanzees range at Mt. Assirik?
3) What are the sizes of groups occurring?
4) What is the density of chimpanzees at Mt. Assirik?

The questions will be discussed with reference to other populations of chimpanzees.

The data used in this chapter come from a variety of sources, principally from the direct observation of chimpanzees and from records of their nests, over the course of 28 months, February, 1976 - June, 1978. In some cases estimates have been made for comparison with other populations of chimpanzees, but the aim in estimation was to be as explicit and accurate as possible. A greater reliance is put on data from nests because the method of collection was regular and systematic. Direct observation of chimpanzees was mainly fortuitous.

2. The usage of different types of habitat and seasonal variation:

Introduction

In Chapter 4, the vegetation of the study area was classified broadly into 5 types: gallery forest, woodland, grassland, bamboo and plateau. This classification will be used to describe the usage of habitats by chimpanzees.

Chapter 4 showed that the Mt. Assirik region has comparatively little surface area covered by gallery forest, and that in other habitats where chimpanzees occur, small areas of gallery forest always have coincided with large areas of woodland. In such habitats, chimpanzees chiefly use the gallery forest, but may use woodland seasonally: Suzuki (1969) described how chimpanzees in the Kasakati Basin, Tanzania, moved into areas of "open forest" and "dry woodland" at the end of the dry season to feed on seeds and drier fruits found there. For the rest of the year they were concentrated in forest and "thicket" areas. The chimpanzees at Mt. Assirik might do the same: there are hard and soft seeds, which are high in protein, forming in some woodland species at the end of the dry season, e.g. *Afzelia africana*, *Parkia biglobosa*. In addition many deciduous woodland species have flushing leaves at that time: these are generally higher in protein and more easily digested than mature leaves (Hladik, 1977). Seasonal differences, however, exist not only in the distribution of food, but in other factors which may affect the types of vegetation which chimpanzees use. During the dry season, trees in woodland shed their leaves, whereas in the forest on a small proportion of trees are bare at any one time (see Ch. 5). Where there is more shade, there will be lower air temperatures. Moreover it is only in some forested areas that water is found. These factors might discourage chimpanzees from using the woodland, despite its resources of food.

Even if chimpanzees were able to make use of woodland as well as forest, these two types of vegetation combined are proportionally smaller than for any other chimpanzee population (see Ch. 5). Thus chimpanzees may be forced to exploit types of vegetation, e.g. grassland or bamboo, where food is scarcer, and which are not used elsewhere. If this is the case, then it could affect the distance over which chimpanzees range: they might have to cover more ground to reach a sufficient number of food-bearing trees, as trees are more widely scattered in these types of vegetation. The vegetation may also affect social organisation: at Gombe, female chimpanzees and their unweaned offspring tend to have smaller individual ranges than do males (Wrangham, 1975). Presumably they are hindered in movement and prefer not to travel widely; these restrictions do not apply to males. Perhaps at Mt. Assirik, however, the vegetation cannot support chimpanzees with small ranges: thus females will be forced to travel over large areas, along with males.

3. The usage of vegetation: results.

The results presented in this section show the types of vegetation that are used, and the seasonal variation in this usage. The data came from two sources. The most direct method was observation of chimpanzees in a given habitat. For every observation, the type of vegetation in which chimpanzees were first seen was recorded. The data presented here were collected by this method from February 1976 to June 1978, a total of 28 months (August, 1976, excepted). The second source of the results is the record of the locations of nests from June 1976 to May 1978. Every nest seen while searching for chimpanzees was noted by its location, estimated age and the species of tree (unless it had already been recorded). Ideally, nests were recorded soon after they were built, but if an area had not been visited recently, the nests recorded could be of all ages (the method for estimating age is found in Chapter 4).

The frequency with which we found these kinds of evidence in the different types of vegetation should be compared with the amount of time spent searching them. This has been neglected by other researchers, e.g. Izawa & Itani (1966); lack of this information makes it difficult to interpret the results from locational evidence of chimpanzees. That is, concentrations of nests in certain types of vegetation could reflect the observers' biassed searching, and not the chimpanzees' preferences.

Unfortunately, at Mt. Assirik, researchers did not record the absolute time spent in each type of vegetation, so a method was devised to assess the proportions of time spent in each habitat. Time, rather than distance covered, was chosen as the parameter because on the whole it seemed more likely to increase the probability of hearing calls, observing chimpanzees and finding their traces. Hearing and seeing chimpanzees was often a matter of luck, but finding traces tended to be related to the thoroughness with which we looked and smelled, and this was related to time rather than distance.

A sample of 253 chimpanzee searches from March 1976 to March 1977 inclusive was taken. The number of months totalled 12 (August excluded). These were divided by the seasons: dry season (4 months), transitional dry-wet (April and May), wet season (4 months), transitional wet-dry (November and December). These divisions were chosen to match other analyses; it was not known if any seasonal differences in chimpanzee behaviour would be abrupt or gradual, so the finer distinction of transitional months was made.

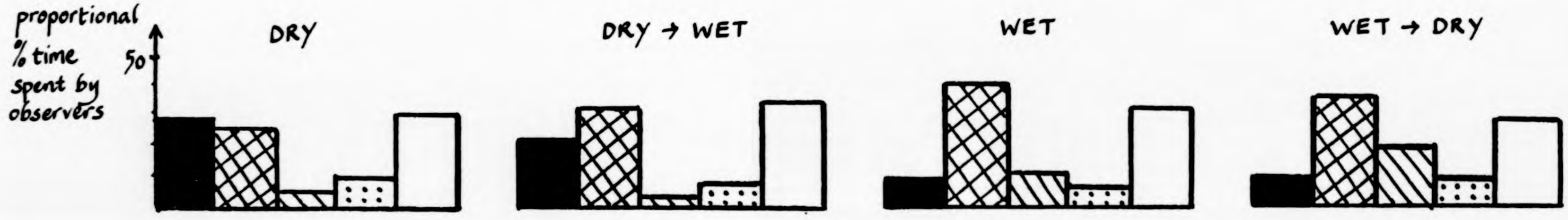
For each search, the types of vegetation were rank-ordered by time spent in each. The type in which most time was spent was given a value of 5, and the others were given whole numbers down to 1, which was least. If a type of vegetation had not been entered during the course of a search, it was given the value of 0. The totals of these scores for each type of vegetation in a season's sample were expressed as percentages of the total rank scores for that season. The search strategies used in these samples were typical of our searching each year.

The results are shown in the first histogram in Fig. 1. It can be seen that the proportions of time spent were not the same as the actual proportions of vegetation types (see pie chart, Fig.11 in Ch. 5). Plateau and woodland areas were searched throughout the year in proportionally as much time as one would expect by chance from their areas (each about 30%). Forest, however, had proportionally much more time devoted to it than its surface area would suggest, in the dry season and at the change from dry to wet. Grassland and bamboo were neglected throughout the year, although they were best searched in the months between the wet and dry seasons.

Throughout the year, about 30% of the time spent on searching was on plateau. This was not because we expected to find chimpanzees there, but because by walking on the edge of plateaux we could walk without impeding vegetation, at the same time scanning adjacent habitats, both aurally and visually.

Finally, it is important to note that our campsite was situated on the

Figure 1. Seasonal variation in proportional time spent by observers in each type of vegetation.



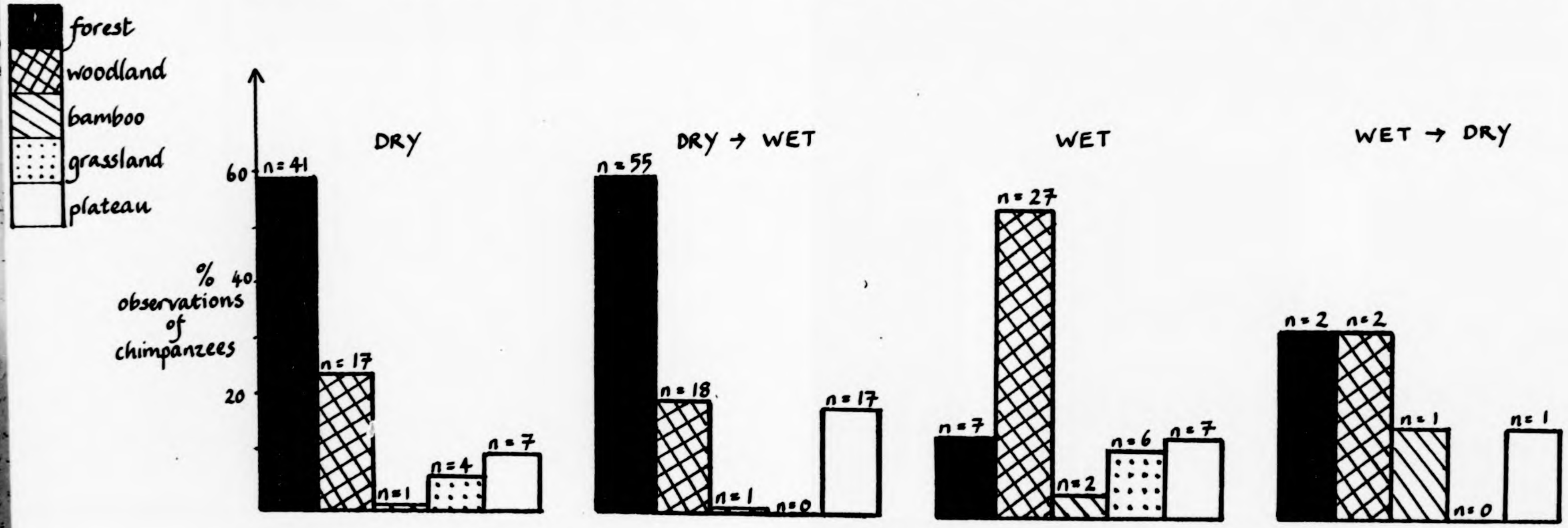


Figure 2. Seasonal variation in observations of chimpanzees in each type of vegetation.

Table 1. The distribution of nests by season and type of vegetation.

Season	Nests	Months	$\bar{X}$ Nests	Forest		Woodland		Grassland	
	N	N	per Month	n	%	n	%	n	%
Wet	600	9	67	88	14.7%	398	66.3%	114	19%
Wet-Dry	860	4	215	114	13.2%	583	67.8%	163	19%
Dry	816	6	136	324	39.7%	446	54.7%	46	5.6%
Dry-Wet	603	4	151	409	67.8%	192	31.9%	2	0.3%
TOTAL	2879	23	125	935	33%	1619	56%	325	11%

edge of a stretch of gallery forest, so that the time spent in camp all year round boosts the relative proportions of time spent monitoring forest in relation to the other habitats. The possible effect of this will be discussed with the results.

The proportional time spent in each type of vegetation can now be taken into consideration when looking at the results of direct observations of chimpanzees in Fig. 2.

It can be seen that the Figs. 1 and 2 are not congruent. The two should not be tested statistically because the proportions of time in each habitat are general guides abstracted from a crude rank ordering, whereas the observations are nominal data. It can also be seen that in the transitional months, November and December, between the wet and dry seasons, there were only 6 observations, 2 in 1976 and 4 in 1977. Chimpanzees were particularly difficult to find at that time. The differential habitat usage should be ignored for that transitional season, since the number of observations is so small.

The differential use of forest and woodland can be seen clearly in Fig.2: in the dry season, and during April and May, the transitional months at the end of the dry season, chimpanzees were seen mainly in forest areas (59% and 60% of observations), and to a much lesser extent in woodland (24% and 20%). A comparison with Fig. 1 shows that in the dry season, forest was more extensively searched than woodland, but in the transitional months at the end of the dry season, the reverse was true. Thus, the more frequent observations of chimpanzees in forest during the transitional months cannot be a product of our searching strategies.

During the wet season, chimpanzees were seen more frequently in woodland than in forest areas. The searching time was also concentrated in woodland, so that a preference for this habitat cannot be confirmed.

There were sightings of chimpanzees on plateaux throughout the year.

Chimpanzees were always seen on the edges of plateaux: they used the borders for convenient travelling routes, as we did. The one exception observed was when they crossed a stretch of 100m of open plateau as a short cut between one area of forest and another. The proportions of observers' time spent searching plateau were similar all year round, yet most observations of chimpanzees on the edge of plateaux occurred during the months of April and May, also the months in which forest was most used. The use of plateau edges by chimpanzees is probably most advantageous when they are passing the most dense vegetation (i.e. forest).

The effect of our proximity to forest when in camp is not thought to alter the pattern of data on habitat usage. In the dry season, the use of forest is probably exaggerated, but there must be a difference between seasons, since the camp remained in the same place.

So far, the limited data suggest that chimpanzees prefer to use forest rather than woodland during the middle and late dry season, but that during the wet season they prefer woodland to forest. Little is known of their use of vegetation at the beginning of the dry season, when they were rarely found.

The systematic recording of chimpanzees' nests in the study area is a reliable source of evidence for the usage of vegetation by chimpanzees. Nests are more easily seen than chimpanzees since they are almost always high up in tress (see Ch. 9), and they usually remain in place for several months. Thus the time spent by observers in each habitat is not a biassing factor. Of course, this evidence shows which habitats were used at night, for nesting, and this is not necessarily the same as daytime use of vegetation for feeding, travelling, etc.

Two years' data from June 1976 to May 1978 are presented, with all calendar months included except August 1976. Since the method of recording allowed all nests to be noted if they had not been recorded already,regardless of their age, nests made in August were found and recorded in the following months. Thus, all nests made in the study area were recorded if seen, even if there was sometimes a delay.

On average, 125 nests were recorded per month. The two months with the highest number of nests were January 1977 (N = 337) and January 1978 (N = 432). In both these months, chimpanzees were rarely found: the vegetation had by then died down, making walking and visibility easier. Researchers roamed further and further afield, looking for chimpanzees. In the course of this extensive searching, rarely-visited or new areas were examined, and a count of all old nests, not previously recorded was made. Thus, large numbers of nests, which had been made in the preceding months, were discovered in January, a middle dry season month.

The results are presented in Table 1. Of the types of vegetation, only forest, woodland, and grassland are tabled because during this period, no nests were found in bamboo or plateaux areas. (Outwith this period, one nest was found in a tree on a plateau). In Chapter 5 it was found that trees occurring in bamboo are widely spaced and tall, often with water-storing properties, e.g. Borassus sp., a palm not suitable for nesting, or the baobab (Adansonia digitata), which is leafless throughout much of the year. Nests were not found on plateaux because trees rarely grow there.

Most nests were found in woodland. This is the case for all seasons, except at the end of the dry season. Overall, more than half the nests found (56.3%) were in woodland, 32.4% were found in forest, and 11.3% were found in grassland. A breakdown of the percentage of nests in each habitat, per season, shows a variation (see Table 1). During the wet season and the early dry season, most nests are made in woodland, then in grassland and finally in forest. Over the course of the dry season this pattern changes; woodland nests are still most common, but in second place are forest nests, while grassland drops to third position. By the end of the dry season, forest nests are most common, with woodland second and grassland negligible.

An interesting point emerges when these findings are compared with the data from direct observations. The seasonal pattern of habitat usage is very similar, with the exception of the middle of the dry season. At this time of year, chimpanzees are seen most frequently in the forest by day, yet it seems that they nest most frequently in the woodland. There are several possible explanations for this: one involves air temperature. In the wet and early dry seasons, chimpanzees can spend any amount of their time, day or night, in the woodland and grassland areas. As the dry season progresses, air temperatures rise, and chimpanzees prefer to spend the daytime in forest, benefiting from cooler air temperatures (see Ch. 3). They move into the more open areas of woodland when temperatures fall, in order to nest. They may also feed there in the early morning and late evening. By the end of the dry season, they tend to spend both day and night in the forest. This could be because water has become extremely scarce, and chimpanzees are reluctant to travel far from the few remaining forest water sources. The seasonal usage of types of vegetation may be related to air temperature and the distribution of water, as indicated, or to patterns of feeding. Chapter 8 suggests that it is not the availability of food which affects these movements, but the possibility remains that it is a particular dietary need for certain elements in foods (e.g. water content or minerals) which guides them. A combination of factors may be responsible.

The finding of nests in grassland is important. It strengthens the evidence of usage, which came from our 10 observations of chimpanzees in grassland over 2 years (see Fig. 2). This has not been recorded elsewhere. In Kano's survey of chimpanzees on the eastern shore of Lake Tanganyika, he noted that neither grassland nor savanna were used for nesting, although chimpanzees had been seen to pass through these types of vegetation on rare occasions (Kano, 1972, pp.114-115). At Mt. Assirik, the use of grassland appears to be seasonal. In the middle of the dry season, only 5%, and at the end of the dry season, only 0.3%, of nests were found there, whereas in both the wet and early dry seasons 19% of nests were found in grassland.

This constitutes a considerable use of grassland, albeit seasonally. In the wet season it is more heavily used for nesting than the forest. This shows a unique adaptation to the distribution of vegetation at Mt. Assirik.

Finally an explanation must be given for the seasonal variation in the number of nests found per month. Nests were found least often in the wet season. This is thought to relate to the ranging of the chimpanzees. In the middle and late dry seasons, water is restricted to certain places in the study area, and chimpanzees are probably limited to staying within access of the water sources. In the wet and early dry seasons, water is available everywhere, and chimpanzees are free to travel wherever they will outside the study area.

The availability of water would explain why the seasonal usage of habitats at Mt. Assirik is different from that found in the only other similar habitat which has been studied in detail - the Kasakati Basin, Tanzania (Suzuki, 1969). There, the use of forest decreases in the dry season when chimpanzees move into the woodland to forage for grains and seeds. Neither Suzuki (1969) nor Kano (1972) described the availability of water there, but since it was not mentioned as a significant factor in ranging behaviour, it is unlikely to be one. The usage of habitat types and seasonal variation will relate to the next section - ranging.

4. Ranging

This section will be concerned principally with assessing the size of the home range used by chimpanzees at Mt. Assirik. Home range is defined as the total area used annually by members of a community. Community is used here to mean a group of chimpanzees, acquainted with, and tolerating one another, and sharing a common home range. They may never be seen together all at once, but variable and temporary sub-groupings occur. Community is the term used by Goodall (1975), but other researchers have used different names for the same concept: group (e.g. Reynolds and Reynolds, 1965), unit-group (e.g. Nishida, 1968), pre-band (Itani and Suzuki, 1967), and regional population (Sugiyama, 1969). The temporary association of chimpanzees within the community is here termed a party, after Sugiyama (1969), but this association has been called a group (e.g. Goodall, 1965), band (Reynolds and Reynolds, 1965), nomadic group (Suzuki, 1969), and small-sized group (Izawa, 1970). The ranges of individual chimpanzees, within the same community, differ; the home range of the community involves the collective mapping of these areas. Finally, it is now accepted that the only constant grouping of chimpanzees is that of a mother and her unweaned offspring. To state definitively the size of a home range, long-term data based on individual recognition are necessary: these can only be drawn from records of each individual's annual range and social relationships. No such data are available from Mt. Assirik. Instead, from pieces of evidence, the best hypothesis can be constructed.

This hypothesis will be constructed from: a) information on the movements of one identified individual over the course of 25 months and another over the course of 28 months; b) the locations of sightings of chimpanzees; c) the movements of groups over the course of several hours.

One-Eyed Sam

We were fortunate, early in the study, to observe an adult male chimpanzee with one easily distinguishable feature. He was seen for the first time on March 24, 1976 and was described as follows:

> "... Male of fully, even brown face, probably prime adult, although aspects of his appearance and behaviour make him seem elderly. His right eye is blind, appears milky-blue-grey in colour like a cataract but bigger area than lens (wall-eyed?)"

He was named One-Eyed Sam. His white eye made him unmistakable, and his unusual behaviour was probably due to his being blind in that eye. He would move his head from side to side when scanning in the distance, presumably to aid depth perception. He also would allow observers to approach to a distance of about 10 metres before showing alarm. He was seen 10 times before his death on the night of 7 May, 1978, and on 7 occasions he was alone.

The first observation was of him feeding alone in a fig tree. He was seen there again on the following day. A group of 14 chimpanzees approached him. The group included 5 adult males, and Sam's behaviour was clearly submissive. He descended, pant-grunting, screaming and bobbing, but was not seen to be attacked. The third observation was made 7 weeks later when he was with another adult male. After that, he was always seen alone except for April 29, 1977, when he was accompanied by adult females and their offspring.

It was just before that, on April 14, 1977, that he was first observed with serious injuries, which were incompletely healed:

> "His scrotum is torn at the back and the skin has retracted up to the leg exposing his right testicle which is dark pink ... There are a number of scars on his buttocks and lower back and one gash on his upper leg ... The knuckles on his right hand are damaged, and there's a big chunk missing from one. He is somewhat skinny but has a big belly."

When observed on January 30, 1978, he was feeding on figs in an area of grassland. The next time that he was seen was May 7, 1978, in gallery forest. He was in a pitiful condition. He was emaciated and had more partially healed wounds; his right ear was almost torn off; he had a finger missing and a deep wound in his left calf. He was scarcely able to walk from the day nest he had made to a small pool of murky water closeby (see Fig.3). He appeared to be almost completely blind and was surrounded by flies.

The following morning we found him dead beside the pool of water. He was

Figure 3. One-Eyed Sam, the day before he died.

lying on the ground in a sleeping position with his eyes closed.

From this story, it is clear that although we have information on the range of One-Eyed Sam, he should not be considered as a typical adult male chimpanzee. His blindness appeared to be a handicap, and must have put him at a disadvantage with other adult males. Other chimpanzees were probably responsible for his wounds, since the large predators at Mt. Assirik probably would have killed him outright, had they attacked. It is probable that he avoided other chimpanzees and because he was handicapped, his range was smaller than that of other chimpanzees.

The map in Figure 4 in Appendix I shows the furthest points at which Sam was observed (blue line). They are joined together by paths which avoid the open plateaux(as chimpanzees have never been seen to cross large expanses of plateau). Sam's minimum projected range, avoiding plateaux, is $8.87km^2$.

The data come from 25 months of this study. During this time most of his range was regularly searched. The fact that he was seen only 10 times suggests to us that he was outwith the ranges marked in Fig. 4 for much of that time.

Brown Bear's range

A second adult male was identified and observed in five locations from September, 1976 to December, 1978. He is a prime adult male with brown face, a notched right ear, and a noticeably brown back. He was named Brown Bear and his range is shown in red on Figure 4. Although he is much more likely to represent typical ranging than Sam is, Brown Bear's known locations number only 5, and his minimum range ($6.68km^2$) is less than Sam's.

Sam's and Brown Bear's projected ranges ($8.87km^2$ and $6.68km^2$) are smaller than the average adult male's at Gombe National Park ($12km^2$), the only site with comprehensive information on individual annual ranges (Wrangham 1975). The two sets of data are very different, however. In Wrangham's study, the average number of observation points for each subject was 795; there were 9 subjects, all in good health. There are 10 and 5 observation points for Sam and Brown Bear respectively; there are only 2 subjects, and one was physically handicapped, his condition deteriorating over 25 months through injury and increasing blindness. The average annual range of adult males at Mt. Assirik is expected to be much greater than both these. What is important from the observations of Sam and Brown Bear is the connection between them. Although limited, the observations represent two overlapping ranges (see Fig. 4) which strongly suggest that the two chimpanzees are members of the same community.

Other Sightings of Chimpanzees

The locations of observed chimpanzees are shown in Figure 4 (App. I). These are indicated by purple dots; movements are indicated by solid, purple lines. The range of One-Eyed Sam is shown in blue, and of Brown Bear in red. The figure is designed to show any clusterings of observations in a given area and to show how routes used by chimpanzees may be connected. Assuming the basic social organization of the community (see discussion of density), where travel routes connect, we can tentatively state the continuous range of one community, especially when this is supported by the continuous occurrence of nests. (See Fig.4). Large gaps where no observations, calls, or nests occurred despite regular searching indicate that the area is not used by chimpanzees and may be a barrier, or even a gap, between two separate ranges.

Lines pass through, and extend out of Sam's and Brown Bear's ranges. If the farthest-flung observations points are joined by the shortest distances (green line), the area contained within measures 42.3km^2. Nests (black dots) were common throughout this area, except on plateaux and some areas of grassland; in some directions (NE and SW) nests continued outside it. Heavy concentrations of nests occurred in Lion Valley and on the slopes of Mt. Assirik, where many observations also occurred, but there was also a concentration of nests in the Acorn Place and New Valley region where only 1 observation occurred. This latter area of nest concentrations straddles the drawn range line of the community, based on direct observations. At Mt. Assirik, then, I propose a single community range of at least 42.3km^2. As will be shown later, it is probably very much larger than this.

This proposed range is larger than any other found at sites where chimpanzees are habituated. In fact, large home ranges have been found only in areas where the chimpanzees were unhabituated, and the evidence was circumstantial (Suzuki, 1969; Izawa, 1970; Kano, 1972). A case could therefore be made that large ranges are an artifact of lack of direct observational data. If this were true, Mt. Assirik might be a similar case, but the assumptions made here have been consistently conservative and are supported by empirical evidence. Moreover, we might expect habituation to be difficult in wide-ranging chimpanzees. A large home range at Mt. Assirik is not surprising, given the small proportions of gallery forest and woodland. Chimpanzees have to cover more ground in the course of a year in order to obtain sufficient food from the sparse vegetation.

Mention must be made of the ranging as it relates to the geography of the study area. From the results, it appears that Lion Valley and Mt. Assirik are most heavily used. Since searches always began and ended in Lion Valley, perhaps observers saw more chimpanzees there because of their great familiarity with it. There are, however, other explanations. The largest continuous area of gallery forest is Stella's Valley (see aerial photograph in Fig. 5). It also has the most permanently flowing and clear water. The next best valley in these terms is Lion Valley. After that, permanent water occurs in Secret Valley, off the photograph, (small amount of clear flowing water); Elephant Rib Valley (flowing but murky); Assirik Valley (few small pools of standing water); the lower reaches of New Valley (small amount of clear, flowing water); Cross Valley, off the photograph, (few small pools of murky water); and Orange Baobab Marigot (one puddle, 50cm x 50cm, dirty).


[illegible] owing Mt. [illegible]sirik,
Mt. Assirik

Figure 5. An aerial photograph showing Mt. Assirik, and valleys which have permanent water.

Figure 5. An aerial photograph showing Mt. Assirik, and valleys which have permanent water.

New Valley

These descriptions of water are for the end of the dry season, when availability is most restricted. Density of vegetation is roughly proportional to amount of water. We might expect usage of the forests to be proportional in the same way. A factor operating against this was the presence of the Rehabilitation Project in Stella's Valley (Brewer 1978). Although the camp was small and had only 2-9 chimpanzees there at any one time, it is thought to have affected the ranging of the wild chimpanzees. They still use the valley, but apparently less so than when the project first began (Brewer, pers. comm.) and less than one would expect from the amount of forest there. Interactions between wild chimpanzees and those belonging to the project have ranged from friendly to aggressive, but since April, 1978, wild chimpanzees have 3 times approached and attacked the rehabilitates at the project's camp-site. This may be an attempt to regain part of their former range.

Otherwise, use of the various stretches of forest would seem to be proportional to the amount of water and forest vegetation, with the exception of Elephant Rib Valley. There the water is murky but expansive, an estimated 30m^2, but only two nests have been seen there during the whole study. This could be because it is accessible only by crossing an open area of grassland, or through bamboo thicket; but it is more likely to be the boundary of the range at that side. The park to the northeast of Elephant Rib Valley has much higher proportions of bamboo and grassland than the study area.

The heavy usage of the area of grassland, Acorn Place, is thought to be due to an abundance of "acorn" trees, <u>Diospyros mespiliformis</u>, and big-fig trees, <u>Ficus vallis-choudae</u>, growing there. These had ripe fruit over the course of Oct-Dec. 1976. It was not used to the same extent in the following year, although the abundance of fruit occurred again.

5. <u>Day range</u>

Our limited data from direct observation of chimpanzees prevents us from stating an average day range for the chimpanzees at Mt. Assirik. One could construct an estimate based on evidence from short observations and calls; but there is a risk in relying on calls. Given the flexible social system of chimpanzees, which has been established elsewhere (Goodall, 1965; Reynolds and Reynolds, 1965; Nishida, 1968), one cannot assume that a party of individuals remains stable. Calls cannot be assumed to come from chimpanzees that were recently seen moving in that direction: they may come from a subsection, or from an expanded party.

Certain conclusions can be drawn about movements over the course of a day. At the end of the dry season, Lion Valley, with its permanent, flowing water, was used frequently. Sometimes a party of chimpanzees would arrive at dusk, nest there and then leave at or before dawn the following morning, e.g.:

On 3 May 1978, a large party of chimpanzees arrived from downstream at dusk and nested by camp. Another, small party nested 400m upstream. The following morning they joined and were followed a distance of 2.2km up to woodland slopes at the top of the mountain where the observer lost them at 0925 hrs. The same day, in the evening, a second observer counted a party of 20 chimpanzees of very similar composition travelling down from the mountain. It arrived at the most upstream point of permanent water in Lion Valley and nested there. The following morning the party left at dawn. For 45 minutes, a sub-grouping of the party was followed southeast for 1km into open areas of woodland and grassland before being lost by the observer.

By the end of the dry season, day ranges seemed to be quite long: there were few remaining water sources, (in the gallery forest), and it is hypothesised that these had to be visited regularly. When a common forest species came into fruit, there was a localised source of abundant food, but presumably chimpanzees needed more in quantity or variety of food and had to forage elsewhere, especially if a staple forest fruit failed, e.g.

Pseudospondias microcarpa. This species gave abundant fruit in April, 1977, but in April, 1978, the crop failed, probably through drought, and the forest was not used as much. In 1977, there were 24 observations and 135 nests in April in Lion Valley, in 1978 10 observations and 100 nests.

By contrast, in the rainy season chimpanzees could obtain water anywhere, so that movements over the course of the day need not be governed by the search for water. Chimpanzees could range anywhere that food was available. At this time of year they sometimes spent long periods of time feeding in one place, e.g.

On 27 September, 1976, a large party of chimpanzees was found feeding in the grassland of Buffalo Valley at 16.31 hours. They fed until dusk, then nested in the same place. The following morning we observed them from 0635 until 1150, by which time they had moved no more than 300m from the nesting site.

It seems likely that the length of a day range will vary seasonally. In the wet season it will be shorter than in the dry season when the need to forage and find water will involve longer daily journeys. As yet, the data are not sufficient to test this.

6. Party Size

It has been found in several habitats (Goodall, 1965; Reynolds and Reynolds, 1965; Izawa, 1970) that the social organization of wild chimpanzees is flexible within the membership of one community.

Variation occurs in the size of the basic community, the area that it uses, and in the size and composition of the temporary parties forming within the community. The possible factors affecting temporary parties are thought to be the distribution of food (which is likely to vary seasonally), the presence of oestrous females and individuals' preferences for companions.

Izawa (1970) compared the size of temporary groupings within a community in three different studies by classifying observed parties into those of 7 or more individuals, and those with 1-6 individuals, excluding carried infants. His data are presented in Table 2, with the addition of comparable figures for Mt. Assirik. The figures for Mt. Assirik come from counts of the number of individuals present when the observer had no evidence that any others were also present.

The results for Mt. Assirik, including counts when the observer counted all visible chimpanzees, but thought more were present, are naturally skewed even more heavily in favour of small groups: 83.5% < 7, 16.5% > 7, $N = 224$. In either case the figures closely resemble those found by Goodall (1965).

The distribution of party sizes observed at Mt. Assirik is shown in Fig.6. Only figures for counts thought to be complete are given, $N = 178$. Carried infants are counted as individuals.

As the histogram shows, large parties are rarely seen at Mt. Assirik. Of the 178 accurate group counts, only 6 were parties of more than 15, including infants. The largest party ever seen was 21, compared with 69 in the Budongo Forest (Suzuki, 1971), 43 at Filibanga (Itani and Suzuki, 1967) and 29 in the Gombe National Park, Tanzania (Teleki, 1977).

The average size of the Mt. Assirik parties was 4.6 (range: 1-21) ($\bar{x} = 4.56$, $N = 151$, dry season; $\bar{x} = 4.69$, $N = 27$, wet season): this compares with 4.2 (range: 1-29) at Gombe (Teleki 1977).

Party size has been thought by many (e.g., Azuma and Toyoshima, 1962; Reynolds and Reynolds, 1965; Wrangham, 1975) to be related to the distribution of food. Large parties have been observed at a source of abundant food. At Mt. Assirik the vegetation is comparatively sparse, and thus food is generally widely distributed. One would therefore predict smaller party sizes.

Factors which might operate in the opposite direction are the dangers presented at Mt. Assirik by large carnivores, and the possibility of competition

Figure 6. The distribution of party sizes.

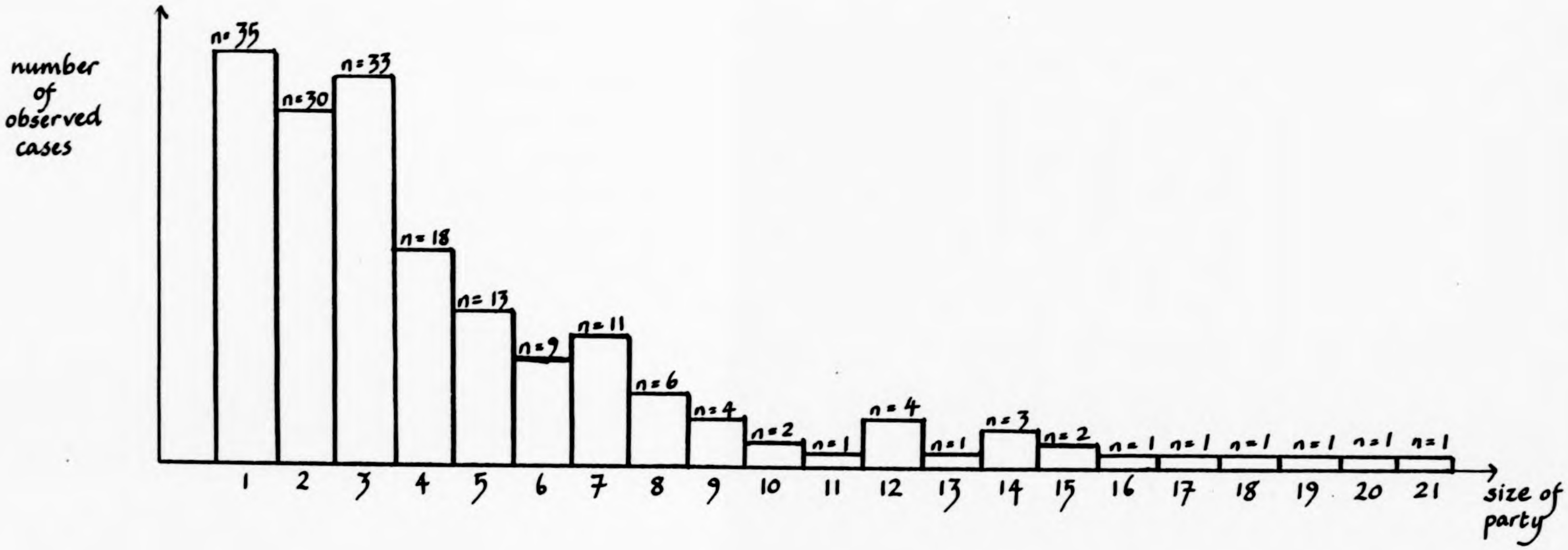


Table 2. The frequencies of party sizes observed in four different studies.

Size of party	Reynolds & Reynolds (1965)	Goodall (1965)	Izawa (1970)	This study
$N \geqslant 7$	38.1%	18%	32.7%	22.5%
$1 \leqslant N \leqslant 6$	61.9%	82%	67.3%	77.5%
N	215	498	107	178

over a food source with large groups of baboons. Larger sizes of parties would increase the safety of chimpanzees moving about the region, and their strength in competition. If the mode of adaptation to these possible threats is not size of parties, it may be one of composition of parties, and this will be discussed in Chapter 7.

7. Density

The term density has been used indiscriminately by authors to mean both the number of chimpanzees in a community divided by the size of their home range (e.g. Sugiyama, 1968), and to mean the total number of chimpanzees in a regional population divided by a large surface area in which one or more communities may live, with or without overlapping ranges (e.g. Kano, 1972). Sometimes both may be given (Goodall, 1965). Sometimes no definition is given and both kinds of density are lumped together (e.g. Wrangham, 1975). Such differences in definition render comparisons difficult. My interest is in the first definition of density: the surface area used by a community of chimpanzees divided by the number of its members.

Clearly, to arrive at a figure for this density, one needs to know the size of the home range and the community. We were not able to confirm either of these. The next best information must be an estimate of density, based on estimates of the range and the size of the community.

First of all, what evidence is there that the chimpanzees seen at Mt. Assirik all belong to the same community? One indication is that, with the exception of areas without trees, there are no large gaps in nest distribution within the minimum range described earlier (see Fig. 4). Secondly, in other studies of chimpanzee communities, on boundaries between community ranges, patrolling behaviour by adult males of one community has been observed (Goodall et al., 1979). As will be shown in Chapter 7, such all-male groups have not been seen at Mt. Assirik. Thirdly, on occasions when a mixed group has been under observation, and calls from other chimpanzees have been heard, the behaviour of the observed chimpanzees has always been similar to that described by Goodall (1965, p.457) for intra-community contact rather than that described by Wrangham (1975; Ch. 5) or Nishida and Kawanaka (1972; p.145) for inter-community interaction. In conclusion, it seems that within the study area, only one community has been observed.

To estimate the size of the community is difficult. The largest number of chimpanzees ever seen together was 21, but studies elsewhere with individual recognition of chimpanzees (e.g. Sugiyama, 1968; Wrangham, 1975) have never found all members of one community to congregate together at the same time. In a variety of habitats, the largest parties observed have been thought by researchers to represent various percentages of the community size: 60% (Sugiyama, 1968) in Budongo Forest, 64% (Teleki, 1977)in Gombe National Park, 81% (Suzuki, 1971) in Budongo Forest, and 100% (Itani and Suzuki, 1967) at Filibanga. (Percentages are reckoned from published figures of party and community sizes). Thus, if 21 is the largest observed group, it is the possible minimum size of the community and 35 (60% of 35 = 21) is the estimated maximum.

Concerning chimpanzee range, it was shown earlier in this chapter that the minimum size for this is 42.3km^2. Thus, there are the means to estimate the <u>greatest</u> possible density of chimpanzees at Mt. Assirik:

$$\text{Density} = \frac{35 \text{ chimpanzees}}{42.3\text{km}^2} = 0.83 \text{ chimpanzees/km}^2$$

This maximum figure does not agree, however, with an estimate of density based on nest counts within the minimum home range. As mentioned earlier, all nests were recorded sooner or later. An underestimate in the number of nests could occur from the observers' not searching all areas often or thoroughly enough, or from chimpanzees' re-use of nests, which we know does occur (see Ch. 9). An over-estimate could come from an observer recording a nest which had already been counted, or from a chimpanzee's making more than one nest per night, which we have also observed (Ch. 9).

These errors probably cancel each other; it seems likely that our counts represent the actual number of nests made.

Annual totals for recorded nests are as follows:

June, 1976 - May, 1977 (inclusive	=	1479
June, 1977 - May, 1978 "	=	1355
		2834 nests

This gives a mean of 1417 per annum. If the mean of the 2 years is divided by the number of nights in one year (N = 365), the results represent the mean number of independent individuals making nests in the study area on any one night. This is 3.9.

The minimum community range is 42.3km^2. Thus the average annual density within this area is reckoned as:

$$\frac{3.9 \text{ chimpanzees}}{42.3\text{km}} = 0.092 \text{ chimpanzees/km}^2$$

The two estimates of density differ by a factor of 9+. This second, lower density is preferable because of the more systematic nature of the data from nests. If it is the true density for that area of 42.3km^2, then the estimates of the size of the community must be reduced to 3.9 or else the range must be greatly expanded. Since the community is at least 21 individuals, the estimate of range must be enlarged. For a community of 21 individuals, their estimated range would be:

$$\frac{\text{size of community}}{\text{density}} = \frac{21}{0.092} = 228.3\text{km}^2.$$

The larger the community, the larger the home range, e.g. for 35 individuals, their range may be as much as 360.8km^2.

In conclusion, the estimated density is proposed as 0.1 chimpanzee/km^2, the community size is about 25-30 individuals, and their range is about 250-300km^2.

While it is clear that the estimates above are all based on other estimates, and that there is room for error, the estimates have been carefully derived.

Although there are no conclusive data to support them, the proposed low density and large home range agree with our general impressions over the course of the study. Even with our knowledge of food and water resources, of travel routes and nesting sites, all built up over the course of 28 months, chimpanzees are still scarce and difficult to find. Why this is the case and how it relates to their use of habitats will be discussed.

8. Discussion

After a description of the vegetation, (see end of Ch. 5), it was concluded that chimpanzees at Mt. Assirik would have to use types of vegetation not used elsewhere in order to survive. The alternative was to range further in order to cover adequate amounts of forest and woodland. It seems that the chimpanzees of Mt. Assirik use both strategies.

Concerning the usage of habitats, it has been shown that chimpanzees at Mt. Assirik make more use of woodland for nesting than any other type of vegetation. Further study may show that it is most heavily used for all activities. At the moment data from observations are more frequent from forest; this is taken to indicate that it is used more during daylight hours than for nesting. The chimpanzees also make considerable use of grassland areas for nesting, travelling and feeding; this has not been found elsewhere.

There is seasonal variation in the usage of habitats. Forest areas are much less frequently used both for nesting and by day in the wet season than they are for the rest of the year. This is the reverse of the pattern found by Suzuki (1969) in western Tanzania. On the other hand, grassland is used more (at least for nesting) in the wet season and the transitional months than in the dry season.

The usage of the different types of vegetation is thought to be related not just to the density of trees and the distribution of foodstuffs within them, but to the availability of drinking water. This is a critical factor at the end of the dry season, limiting movement away from those forest areas which still have it. During the wet season, however, it is abundant.

Another finding which appears to be an environmental adaptation is the small sizes of parties at Mt. Assirik. The size of the whole community is also thought to be small. This social arrangement is thought to be due to the sparse distribution of vegetation and therefore the wider distribution of food.

In addition to their vegetational versatility, the chimpanzees also range more widely. The estimate of range is 250km^2 for a group of 25 individuals, but the data show that it must be a minimum of 42.3km^2.

Studies of habituated chimpanzees have all produced estimates of home ranges under 40km^2, but these were either forest-dwelling populations (Reynolds and Reynolds, 1965; Sugiyama, 1968; Suzuki, 1971) or populations which were provisioned with food (Albrecht and Dunnett, 1971; Nishida and Kawanaka, 1972; Wrangham, 1975). Forest populations can be expected to have smaller ranges because the distribution of food is more dense. Provisioned populations have been suspected of having reduced ranges because the method provides an additional source of abundant food. Comparisons are best made with savanna-dwelling chimpanzees which are not provisioned. Estimates for their home ranges are larger, although the data are more indirect. The largest estimate comes from Kano (1972) for the Ugalla and Wansisi areas, Tanzania: 470-560km^2 and 250-550km^2, respectively. These involve assumptions, however, which may not be valid. Home ranges were calculated from the total area of a geographical region divided by the estimated number of communities contained therein, assuming that all ranges touch each other. This may not be so, especially in an area of such open vegetation, and since information gathered by Kano from nests and the reports of local people show there to be gaps where evidence of chimpanzees is lacking. This is the case for both the Ugalla and Wansisi regions. The same drawbacks occur with the estimates of ranges given by Suzuki (1969) for the Kasakati Basin: 25-200km^2.

In contrast, Izawa (1970) gave careful estimates based on direct observation with some individual recognition. His estimates for two communities of about 50 and 40 individuals were 122km^2 and 124km^2, respectively. In general, it appears that larger home ranges are necessary in more open habitats.

Ranging at Mt. Assirik also seems to change seasonally. It is not in the nature of a "migration" as described by Nishida and Kawanaka (1972) since chimpanzees are seen at Mt. Assirik all year round, but we found fewer nests within the study area in the wet season than at any other time. The conclusion is that the chimpanzees were frequently outside the study area in the wet season because water was readily available everywhere.

The density at Mt. Assirik can only be a careful estimate based on estimates of the size and home range of the community, and on the density of nests within this home range. The results showed a maximum density of 0.83/km^2, but a more realistic density is the second estimate from nest data. This is 0.092/km^2. Of the densities derived from other long-term studies, where density is defined as the number of members in a community divided by their home range, this is the lowest density of all. Curiously, the only lower density proposed for chimpanzees comes from de Bournonville's short survey of less than a week (de Bournonville, 1967). He did a comparative survey of distributions in Guinea and Senegal, and gave the lowest density 0.05 - 0.1/km^2, for the area just east of Mt. Assirik. Several studies have found densities which fall between the final estimate of density for Mt. Assirik (0.1/km^2) and the maximum of 0.87/km^2, but these studies reckoned density by dividing an estimated number of chimpanzees by the large surface area in which they occurred, ignoring the effect of separate community ranges with the area.

Such a low density is not surprising at Mt. Assirik, considering that they are one of the most northerly communities of chimpanzees. Scattered nests continue north along one streambed to the north-east, but nowhere further north have any concentrations of nests such as those at Mt. Assirik been seen. Though a systematic study of vegetation has not been conducted north of the study area, it seems more sparse. It is possible that Mt. Assirik has just a critical level of density of woody vegetation preventing the chimpanzees from travelling any further north.

This raises the question of the origins of the Mt. Assirik community. De Bournonville (1967) claimed that the Mt. Assirik population were only recent immigrants from south of the Gambia River. The creation of the national park offered a refuge to chimpanzees which, although existing in a more hospitable habitat before, were hunted by the Bassari and Coniagui peoples. He believed the claim to be supported by information from former officers of the "Eaux et Fôrets" service who maintained that the chimpanzees were recent arrivals. This is disputed by Dupuy (1970), but the Gambia River is passable in the dry season at several points along its course through the park. Sadly, the people who would be able to answer the question are the few villagers who used to inhabit several sites in the vicinity of Mt. Assirik about 30 years ago, but they have long since been moved out and are not easily traced, and no records remain. Judging from aerial photographs, there appears to be a wooded route south from Mt. Assirik to the Gambia River, which chimpanzees could use. Guards have reported occasional sightings of chimpanzees at the southern end of this route. This is the same way used by the few Bassari and Peul poachers who have been seen at Mt. Assirik.

Whatever their origins, the community at Mt. Assirik now demonstrates a unique adaptation to a demanding habitat. Their survival seems to depend on their ability to use vegetation which chimpanzees elsewhere neglect, to adapt this usage to seasonal variation, and to range over a wide area.

Chapter 7.

HEALTH AND SOCIAL BEHAVIOUR

1. Introduction

The purpose of this chapter is to describe aspects of the chimpanzees themselves, principally their health and social behaviour. The chapter is mainly descriptive. Where possible, quantitative comparisons are made with other populations. Nissen (1931) gave a brief description of the appearance and habits of *Pan t. verus*, and it is hoped to elaborate on his work here.

2. Health and Physical Appearance

The chimpanzees observed at Mt. Assirik appeared to be generally healthy. They showed no signs of respiratory infections, e.g., running mucous from the nose, coughing or sneezing, which have been observed elsewhere in chimpanzees (Nissen, 1931; Goodall, 1965), gorillas (Scaller, 1965, p. 99) and orang utans (Rijksen, 1978, p.147). Only two sneezes were heard during the entire study.

The faeces of chimpanzees were usually firm and fibrous. Looser faeces occurred when they had been feeding on large quantitites of figs (*Ficus spp*.) or the soft fruits of *Spondias mombin*.

Only two cases of physical disability were noted. An adolescent female was once seen walking awkwardly. She appeared to have a damaged arm which she held raised as she walked: we do not know if this was permanent or temporary. The second case was One-Eyed Sam (see Ch. 6): the white, opaque appearance of his eye may have been caused by a glaucoma (see Fig. 1). Many adults were seen with minor, healed injuries such as torn ears, missing fingers and toes, and scars. Dark red urine was found spattered on leaves below nests: no record of its frequency was kept, but it was not uncommon. This has been noted before by Nissen (1931) and by Reynolds

Figure 1. One-Eyed Sam in a fig tree: his white eye is plainly visible.

and Reynolds (1965). It may be caused by menstrual blood mixed with urine, or by pigments from plant foods.

The only dying or dead chimpanzees found were a past prime adult male and an old female. Chimpanzees which are injured or unwell probably have difficulty in keeping up with the others. This is suggested by the behaviour of One-Eyed Sam, seen alone 7 out of 10 times, and by the observation of the single old female, first seen in Stella's Valley. She was found dead 3 days after the first sighting, having travelled less than 500 metres. She appeared to have been well into old age. In both cases, the chimpanzees, when dying, remained near a source of water.

The physical appearance of the chimpanzees was noted with interest, in light of the debate over the distinctive external features of the subspecies (see Ch. 1). The masked face and long hair parted in the middle of the head, thought to be typical of Pan t. verus (Napier and Napier, 1967) were frequently seen in young chimpanzees, although no discernable distinguishing features could been seen in adults. Their faces were usually dark, brown or black,,and their heads balding evenly above the brow ridge; but there was great individual variation in both these characteristics. There was less variation in hair colour: most chimpanzees were all black. Grey beards were fairly common, though no meaningful frequency can be stated since observations of faces varied so much in quality. Grey backs were occasionally seen and one prime adult male and one adult female had brown backs. Elsewhere, the occasional reddish-haired chimpanzees have been seen (Nissen, 1931; Reynolds and Reynolds, 1965). Old individuals tended to be lean and had lost some hair from all over their bodies.

3. The Community

The concept of the community at Mt. Assirik was discussed in the section on density in Ch. 6. It is thought to comprise between 25 and 30 individuals. A breakdown of the age/sex classes involved will be attempted by summing them over all sightings. They are grouped by the age and sex classes which we were able to distinguish in the field: since we did not know the life histories of individuals, e.g.. age of weaning, onset of menstruation, we relied on physical appearance and behaviour. Our categorisation was based on physical size, travelling behaviour (dependent or independent), and the state of external genitalia. It agrees with Goodall's classification (1975). Our observation of infants did not often allow us to age them within infancy: their size is difficult to determine from a distance when they are being carried; often only the pink hands, feet and faces show from a mass of black hair. The ventral or dorsal mode of carriage is not a reliable indicator, since it varies in different contexts (see section on mother and infant behaviour later in this chapter). There may also be differences across populations in this behaviour. The distinction between the older infants and juveniles was also difficult since both may travel independently; usually, however, only juveniles will travel independently for long distances. Although old individuals were seen, they are not separated from mature individuals in the data presented here, since they may easily have been underestimated. Only good observation allows a distinction between mature and old individuals and often one could merely state that the individual was an adult. From observations made over 28 months, 205 out of 994 chimpanzees (21%) could not be put into age age/sex category because observation conditions were too poor.

The age classes are presented below with the criteria we used and the approximate age ranges of each class:

INFANT: small, less than about a quarter of adult size; may move independently for short distances while mother is stationary, but is carried when she travels. 0-5 years.

JUVENILE: Larger chimpanzee travelling independently from mother but usually close behind: nests beside her. 5-9 years.

ADOLESCENT: Almost adult-sized chimpanzee, but slimmer in build; travels independently; females may show small sexual swellings and some males show descended testes. 9-13 years.

ADULT: Fully grown chimpanzee; males show fully descended testes and are more heavily built than adolescents; females show full sexual swellings and loose, pink skin in the perineal area when unswollen; females may have offspring. 13 years onwards.

The results are presented in Table 1. It shows that although the sex of infants is not given, where possible it is given for the other age classes. For adult chimpanzees, of which 75% could be sexed, exactly equal numbers of males and females could be recognised: in the other two classes more females were recognised than males. This may reflect the true sex ratio of the younger classes: it was found at Gombe that females predominated in the infant and juvenile classes (Teleki et al., 1976). However, at Mt. Assirik most young chimpanzees could not be sexed (84% juveniles and 57% adolescents), and the slightly higher numbers of females probably reflects the differences in the ease with which male and female subadults can be sexed. In subadults, there is little sexual dimorphism, and when the male's testes are not descended, the female is more easily recognised by her clitoral projection.

One can compare the numbers in each age class to see if they match those one would expect by chance, given a normal population. To do this, some hypothetical assumptions were made about a normal chimpanzee population. Firstly, I assume here that the mortality rate is constant from early infancy until old age. This is the simplest, most parsimonious assumption for an essentially undisturbed population. At Gombe, chimpanzees have a high infant mortality rate (Teleki et al., 1976) but this has not been constant: periodic epidemics have claimed infant victims (presumably because they have less resistance to infection). Since Gombe is the only chimpanzee population for which detailed demographic information has been published, true norms have yet to be established. It is difficult

Table 1. The numbers of chimpanzees falling into each age class (N = 789), with sexes where possible.

AGE CLASS	INFANT	JUVENILE			ADOLESCENT			ADULT		
		♂	?	♀	♂	?	♀	♂	?	♀
Observed age/sex classes	107	7	111	14	19	54	21	171	114	171
Total	107	132			94			456		
Expected totals if life expect. = 30 years	131	105			105			447		

to compute life expectancy for wild chimpanzees: Teleki et al. (1976) showed that this varied throughout life at Gombe; but of those surviving into adulthood (11-12 years), average life-expectancy was a further 15-16 years, i.e., death at 26-27 years. Although one female died at the approximate age of 37 years, mean age of death was 13.5 years.

Table 1 shows the numbers predicted for a life expectancy of 30 years compared with the observed number of cases. The results approximate an average life expectancy of about 30 years. Unfortunately, comparable data from Gombe cannot be added, since raw data on the ages of individuals are not given by Teleki et al. and their age classes are slightly different.

The fact that at Mt. Assirik, the data could come from some individuals seen only once, and some individuals seen repeatedly means that the observed versus expected results should be tested statistically. Although the sampling is thought to be random, at least two possible biases exist. The more obvious one is the effect of the observer, which could cause the shyer adult females and offspring to flee before the bolder adult males. Since almost all our observations were made from concealment, however, this is unlikely to have had an effect. The other possible bias could come from the differential visibility of age classes, e.g. juveniles might be harder to see because they are smaller than adults; but the habitat plays an important part in minimising such an effect because even in the densest type of vegetation, forest, there is little understorey and visibility is good. Once chimpanzees are found, and if they have not been alerted to our presence, they are comparatively easy to see.

Thus the data are considered reliable, and they confirm our subjective impressions that the community is healthy, with no age class more at risk than another. Since chimpanzees in the wild live into their twenties and thirties (Teleki et al., 1976) and females produce living offspring on average only once every 5.6 years, when the preceding child is still alive, any abnormal increases in fatality have a prolonged toll on the population. Thus the distribution of age classes at Mt. Assirik suggest that the population has probably been stable for at least 20 or so years: this picture of a well-balanced population is reinforced by the adult to subadult ratio which is 1.4 : 1.0; this is also the mean of 7 such ratios from different populations presented by Teleki et al. (1976).

4. Parties within the community: their composition

Party sizes were discussed in Chapter 6; the mean size of parties was 4.6 for both the wet and dry seasons (range = 1 - 21).

The composition of observed parties can be compared with those from other populations by using the four types of party classified by Reynolds and Reynolds (1965). These are: MIXED - adults of both sexes with immature offspring; MALES - adult and adolescent males only ; MOTHERS - adult females with dependent young only ; ADULTS - adults and adolescents of both sexes but no juveniles or infants. Single individuals are excluded from this analysis. Data for Mt. Assirik come from the 108 occasions over 28 months when a party could be classified: there were 71 parties discarded because not all members could be put into age or sex classes.

Table 2 shows a comparison of the party compositions found by the five researchers. Except for the Budongo Forest (Reynolds and Reynolds, 1965) the most frequently observed type of party is the MIXED. At Mt. Assirik, 80 MIXED parties (74.1%) were seen. The only researcher finding a higher percentage of such parties was Suzuki (1969). Izawa (1970) also worked in the Kasakati region for periods before and after Suzuki's research, yet his figures for party composition are quite different (see Table 2). There are apparently several communities in the area, and the authors differ significantly in their estimates of the size of the population. Since neither author states which community their samples come from, within

Table 2. A comparison of proportions of observed types of party.

Site	Budongo Forest	Gombe	Kasakati Area		Mt. Assirik
Type of Party	Reynolds & Reynolds (1965)	Goodall (1965)	Suzuki (1969)	Izawa (1970)	This study
MIXED	37.2 %	36.6 %	90.1 %	52.6 %	74.1 %
MALES	15.9 %	12.2 %	1.2 %	7.6 %	3.7 %
MOTHERS	16.7 %	29.2 %	3.2 %	10.3 %	19.4 %
ADULTS	30.2 %	22 %	5.5 %	29.5 %	2.8 %
N	215	350	498	78	108

the Kasakati region, differences in the habitats used by the chimpanzees, or differences in the sampling methods cannot be examined as the possible source of discrepancy. From both reports, it seems that the vegetation in the whole region is of a mixed type so that this factor is unlikely to be a cause of differences between any two communities in their social organisation. For comparative purposes across habitats, the mean of these two sets of results is used here. This gives a percentage of mixed parties in the Kasakati Basin of 71.3%. Thus similar, high percentages of mixed parties come from the two most open habitats (see Ch. 5) - Mt. Assirik and the Kasakati Basin.

ALL-MALE and ADULTS parties hardly occur at Mt. Assirik. A total of 3 all-male parties (2.8%) out of 108 parties were seen and in each case the number of members was only 2. Similarly, parties of adults only were seen 4 times (3.7%) with memberships of 3, 3, 4 and 5. MOTHERS parties were seen on 21 occasions: if it were not for the frequency of this latter type of grouping (19.4%) it could be argued that the mixed party might be a special adaptation to areas with low overall densities of trees. An obvious explanation for this is the potential threat of large carnivores (present in both areas) to parties of chimpanzees travelling in the open; scarcity of trees means dispersion of food and necessitates wider ranging to procure it (Suzuki, 1969). It also means that there are fewer places of refuge. Thus it might be more advantageous for adult males to travel with child-carrying females and immature individuals, at least when in the open areas. If this is the case, then why are not all parties mixed?

A closer examination of the MOTHERS parties revealed that only 11 of the 21 were completely alone. The others all had vocal contact, or the potential for such contact with a MIXED group. Thus the known incidence of these MOTHERS parties being alone is only 10.2%; and most of these (7 of 10) were in forest. This seems to represent a difference between chimpanzees dwelling in open areas on the edges of their distribution

(Mt. Assirik and the Kasakati Basin) and in other more wooded areas. A feature of open habitats in terms of social organisation is the predominance of the mixed party.

Forty-five solitary individuals were observed at Mt. Assirik. Of these, 14 (31%) could not be classified; 4(9%) were adults of undetermined sex; 14(31%) were adult males, 2 (4%) were adult females; 6 (13%) were adolescents (3 male, 3 female) and 5(11%) were juveniles. Lone individuals have been seen elsewhere. Reynolds and Reynolds (1965) maintained that whenever they were seen, others were usually nearby. Goodall (1965) saw 64 solitary chimpanzees out of 498 party sightings (13%); she found lone adult males most frequently, but also adult females and adolescents of both sexes. Izawa (1970) also found lone adult males most commonly (64% of the 45 singletons observed).

It is possible that when solitary chimpanzees were observed at Mt. Assirik, other chimpanzees were nearby. This seems especially likely for the 5 juveniles seen, since they are assumed to be still dependent upon their mothers. Otherwise the most common class of lone individuals, adult males, is in keeping with other populations.

5. Changes and relationships between parties

It has been found elsewhere that chimpanzees join together and split up frequently. This feature of chimpanzee society, however, is difficult to confirm without long periods of direct observation. At Mt. Assirik, one example of fusion between parties was observed in the early morning as chimpanzees left their nests. Two parties nested 0.5 km apart: the larger party moved upstream in the morning along the edge of the plateau towards the smaller party. Members of the latter climbed out of the forest in the gorge onto the edge of the plateau, and all travelled together for 3½ hours. On other occasions we had the strong impression from vocalisations that groups were joining and splitting, but could not confirm this.

Bouts of vocalisations exchanged between parties were the only interactions that we could note often between parties. These occurred when two or more groups were within a kilometre, but could not see each other. Pant-hoot choruses (see section on communication) were exchanged frequently.

6. Locomotion

Chimpanzees travelled quadrupedally on the ground. They were seen moving in this way at all speeds from ambling to fleeing. When travelling in a group, they might move in a tight bunch or strung out in single file.

Bipedal locomotion was seen only once, when an adult male was displaying, but chimpanzees often stood bipedally. They did this apparently to obtain a better view, usually of us. However, on one occasion, a mixed party of 14 chimpanzees crossed an open stretch of plateau, a distance of about 100 metres. They moved in single file, but remained very close together. About half-way across, almost all of the 9 adults stood bipedally and looked out over the vast expanse of plateau. They had not seen me and appeared to be scanning the distance.

The manner in which chimpanzees travelled along the edge of the plateaux was usually swift, silent and vigilant. Often individuals paused to look up and down the plateau edge and out across the open plateau. On one occasion 2 travelling chimpanzees were paying so much attention to the open plateau that they failed to see me sitting on a branch, unconcealed and only 2 metres away. The same thing happened when a group of 20 chimpanzees passed the same place, and the observer was only partly hidden.

By contrast, movement in the wooded areas is slower, probably for a combination of reasons: areas with trees provide safety, chimpanzees are often foraging rather than travelling, and the denser vegetation impedes rapid movement.

7. Communication

Several attempts have been made to describe chimpanzee vocalisations (Goodall, 1965; Reynolds, 1965; Goodall, 1968). These are difficult to compile and compare because of the inadequancy of a verbal language in describing very variable vocalisations. For example, Reynolds and Reynolds (1965), for situations of fear, anger and frustration, named one scream and one squeal and the many conditions under which they occur. They also described a facial expression for each and showed sonograms. Goodall (1965) for situations of fear, named 5 types of scream with their contexts, but did not mention a squeal and did not give facial expressions. These she named scream calls, panting shrieks, squeak calls, screaming and an infantile scream. Clearly, until comparisons can be made of spectrograms or sonograms with accompanying descriptions of facial expression, detailed comparisons should not be attempted. Instead, this section sets out, in general terms, the classes of sounds which have been heard: also listed are a number of sounds named by Reynolds and Reynolds (1965) and Goodall (1968) which are thought to be comparable.

Whimpering

Either a single, or a series of "hoo" sounds varying in pitch and volume. Observed to be made by an infant when temporarily left behind and sometimes when chimpanzees were travelling, probably also because an infant had been left behind. Infrequent. Similar to Goodall's D1, F1, 2 and 3.

Grunts

Exhalations from glottal stops: these may be single or multiple and vary in volume. Soft or medium grunts were observed to be made when chimpanzees approached a food source or were in the course of feeding. Similar to Reynolds and Reynolds' 1 and 2, and Goodall's A1 and 2, B1, 2 and 3 and E2.

A single soft grunt was usually the only vocalisation given when a chimpanzee suddenly saw an observer. This seemed to be an involuntary expression of surprise: it has not been noted elsewhere.

Panting

Fast and repeated exhalations of breath — "haa haa haa haa ...", sometimes accompanied by audible intake of breath. Soft panting, sometimes with grunting, was heard during subadult play: this is similar to Goodall's laughing (C3). Loud, hoarse, panting with loud grunts interspersed was heard from chimpanzees in the presence of a displaying adult male; then bobbing (crouching) gestures sometimes accompanied it, if an adult male approached the submissive, panting chimpanzee. Similar to Goodall's C1 and 2, G1.

Screams

A piercing, shrill, high-pitched call. A wide range of screams was heard from short suppressed squeaks, squeals and single screams to persistent shrill screaming with increasing hoarseness. They were heard following an adult male's display and in conjunction with pant-hoot choruses (see below). Many were heard without the context being determined. Similar to Reynolds and Reynolds" 5, 10, 11, and 12, and Goodall's E5, G2, 3, 5 and 6.

Barks

Barks are short, sudden "waa" calls sometimes repeated. Heard in response to the calls of lion or leopard at night, in conjunction with pant-hoot choruses. Similar to Reynolds and Reynolds' 4, and Goodall's E3.

Wraagh calls

There were rarely heard calls, high-pitched, like the waa barks but longer in duration and more plaintive. Generally heard at night in response to the nearby "coughing" of a leopard.

Similar to Reynolds and Reynolds' 9, and Goodall's E4.

Pant-hoot calls

These usually form a series of calls often rising or falling in pitch. Each call is formed by a rapid, hoarse (sometimes voiced) intake of breath followed by a loud "hoo". Pant-hoot calls can occur in many situations of excitement, e.g., at a source of abundant food, on arrival at a water source, upon nesting or rising in the morning, or hearing other chimpanzees pant-hooting. Similar to Reynolds and Reynolds' 3, 7 and 8, and Goodall's D2 and 3.

Many variations of calls not noted at Mt. Assirik, but described by Reynolds and Reynolds (1965) and Goodall (1968) may have been missed because we had less contact time, or else because there is ambiguity or confusion in the verbal descriptions. One class of sound noted by Reynolds and Reynolds, 6, the soft moan, was not heard at Mt. Assirik. Similarly, the lip-smacking sound made when grooming (Goodall, 1968, C4) was not heard.

The most frequently heard calls were pant-hoots and screams. This may not necessarily be because they are the most frequently given, but because they are among the loudest.

Even when large parties gathered together, however, they gave the impression that there were times when they purposefully maintained silence. For example, when travelling on the edge of plateaux where they were easily seen and did not have the cover of vegetation, they travelled fast, and all chimpanzees were alert and silent.

Vocalisations have been ordered by the types of sound that could be distinguished. The contexts of calls were not used to order them, since in many cases the context could not be determined. The following section will be concerned with gestures and behavioural patterns. For clarity, with the exception of autonomic behaviour, these will be grouped by their apparent function. The data from February 1976 to May 1978 are limited, but I can confirm some behaviours seen in the eastern subspecies. Frequent reference will be made to Goodall (1968). Nishida (1970) also describes the social behaviour and gestures of wild chimpanzees in Tanzania, but the unusual use of English in describing the patterns makes that report a less reliable model for comparison. Other researchers have described behaviour but in less detail, e.g., Reynolds and Reynolds (1965), Sugiyama (1969), Albrecht and Dunnett (1971).

8. Autonomic behaviour

Goodall (1968) lists 3 types of autonomic behaviour: hair erection; penile erection; and the emitting of a pungent odour by chimpanzees during social excitement. Only the first 2 of these have been noted at Mt. Assirik. Hair erection by one or more individuals was seen on 16 occasions, usually in response to suddenly sighting an observer. It was also seen in adult males when they were displaying. Penile erection was seen on one occasion when 2 adult males were travelling silently on the edge of the plateau and a fully swollen female was in the party.

9. Flight and avoidance

Goodall (1968) mentioned flight, startled reaction, hiding and creeping under the heading of flight and avoidance. At Mt. Assirik, chimpanzees fled from observers if they suddenly caught sight of them at close range, but by far the most common response was to leave rapidly but silently.. If they were in trees, they would descend as fast and as safely as possible, then walk briskly, or run away. The startled reaction described by Goodall was not seen: the only indication of surprise was a single, apparently involuntary grunt upon seeing human beings, as mentioned earlier. Hiding was never seen at Mt. Assirik, but we have several indications that to get out of sight of human beings was more important to the chimpanzees than putting distance between them and us. Sometimes a chimpanzee would spot an observer, peer intently for a minute or two, then turn its back to the observer, or else might move just out of sight over the brow of a hill or into thick cover and stay there unless approached again. Creeping was not seen at Mt. Assirik.

10. Frustration or behaviour in uncertainty

None of the behaviours listed by Goodall (1968): self-scratching, yawning, brief grooming, masturbation, rocking, shaking and swaying of branches, charging, slapping, stamping, dragging, throwing and drumming were seen in any situation that could be construed as involving frustration or uncertainty. A number of these behaviours were seen, e.g., yawning, but in other contexts, e.g., lying down in a nest. No temper tantrums or redirection of aggression was seen. The lack of all these behaviours may be due to the comparatively low numbers of contact hours at Mt. Assirik, but a substantial proportion of them noted at Gombe occurred at the artificial feeding area, where frustration and social tension were to some extent artificially increased (Goodall, 1968).

11. Agonistic behaviour

Few agonistic behaviours were observed. None of the behaviours classified as threat by Goodall, (1968) were seen, except on one occasion. A prime adult male, with full hair erection, was pursuing a swollen female through the branches of a large tree above us. He stopped and lay down on a branch leaning against the trunk of the tree. He happened to glance down and saw me beneath him: he stared down for almost 2 minutes, reclining against the tree-trunk, with his hair still erect. Then he made a bluff charge, shaking branches and making repeated, loud barks from the branches above us before he left, following the rest of the party. On all other occasions, chimpanzees left quietly upon seeing us and this male's behaviour was thought to be due to his already excited state.

Although, with this exception, threatening behaviour was not seen, on 11 occasions, components of such behaviour, i.e., charging, swaying and breaking of vegetation, and drumming were heard at close range. Since it could not be seen if an individual was threatened, we assumed that they were parts of displays which may or may not have been individually directed. Four full displays by adult males were seen. On 3 of the 4 occasions, a female with a pink, sexual swelling was present in the party. On the fourth occasion an adult male was seen to charge bipedally down a slope with his hair erect. He threw a rock and shook branches: although other chimpanzees were present they paid no attention to him.

None of the components of attack as described by Goodall (1968) were seen, although attacking charge and stamping on the back were heard. Twice the sound of pounding on the back was heard along with loud screaming. On another occasion there were pant-hoots, followed by crashing through the vegetation, then the pounding on a chimpanzee's back with loud screams.

When any of these threatening or attacking behaviours were heard or seen, there were often loud, frequent, hoarse grunts, pant-hoots, barks and screams from other individuals present.

Submissive behaviour was rarely seen. Most of the behaviours described by Goodall (1968) in this context were never seen. Presenting was only observed when copulation followed. Bobbing was shown by One-eyed Sam when he was approached by a group of chimpanzees containing adult males, and by an adolescent (sex unknown) when it was approaching an adult male. Kissing, non-copulatory mounting and submissive touching were never seen. No reassurance behaviour was observed although there were 5 instances when a chimpanzee reached out to touch another: these all seemed to be cases of casual contact. There were 3 cases when juveniles touched adults (possibly their mothers), 1 case where an adolescent touched an adult and 1 case of an adult touching an infant.

12. Sexual behaviour

Adolescent (*N* = 10) and adult (*N* = 28) females were observed with sexual swellings. These swellings varied greatly. Those in adolescents tended to be smaller and more localised than those of older females. All stages of tumescence were observed. Of the 38 swollen females seen, 33 were definitely confirmed to be in mixed parties: 4 were seen in parties of 4 chimpanzees or more but whose members could not all be categorised: 1 was seen alone. The single swollen female was an adolescent.

As mentioned before, displays were seen, and more frequently heard: many of these occurred when a swollen female was present in the party.

One sexual inspection was seen. An adult male poked his index finger into the vagina of a non-swollen female as he passed by her; he then sniffed his finger. This behaviour was recorded by Goodall (1968). There, mature males tended to inspect non-swollen females, but chimpanzees of ages and both sexes inspected swollen females.

Two matings were seen. The first occurred in a travelling party when an adolescent male turned to face a swollen female which was travelling behind him. He raised an arm, whereupon the female turned to present to him and they copulated. During intromission, she crouched low and the male leaned back on his hands. They followed the rest of the party immediately afterwards. A second copulation was seen when an adult male was sitting in a Saba senegalensis vine. An adolescent female rushed towards him and presented: they copulated, then the female squealed and moved away rapidly. Both these cases are typical of the copulations described by Goodall (1968).

13. Greeting behaviour

We were not able to observe the behaviours described by Goodall (1968) as occurring in greeting, since we did not see parties joining together and splitting.

14. Play

During the 23 periods of observation when play was seen, youngsters from infants to adolescents engaged in a variety of types of play. Twelve times the play was of a social, boisterous kind and involved elements of chasing, hitting and wrestling, accompanied by open-mouthed play faces and laughter (panting and grunting). On one occasion, an infant and 3 juveniles followed one another round a circuit which involved climbing a tree and leaping off a high branch onto the dense foliage of a bush below. They completed 19 rounds before stopping. The next most common type of play, seen 7 times, was solitary locomotor play, e.g., when a lone individual swung or dangled from a branch with a play face, and/or laughter. Solitary play with an object was seen once when an infant with a play face toyed with the empty half of a baobab shell.

In addition, a laughing juvenile was seen to grab at the heels of an adolescent in front of him, as they walked along.

Youngsters were seen to initiate play 4 times, by approaching another with a play face and stamping, dangling legs, or swinging towards the second individual.

On 2 occasions play faces could be seen in young chimpanzees, but the nature of the play could not be determined. In total, 24 juveniles, 7 infants, 3 adolescents and 1 adult were seen to play.

15. Grooming

Chimpanzees were seen grooming on 19 occasions. Most commonly, (15 of 25 individuals) adults were involved, but chimpanzees in all age classes, even an infant, and both sexes were seen to groom. Similarly, chimpanzees of all ages were seen to be groomed. On 6 occasions the grooming was mutual, i.e., both partners actively groomed: 3 pairs of adults, 2 mother-and-infant pairs and 1 pair of adolescents. Two chimpanzees were seen to solicit grooming by approaching another and raising the arm, as described by Goodall (1968: p. 264). In both cases the soliciting chimpanzee was eventually groomed. Whenever grooming was seen, no more than two chimpanzees were involved at the same time.

16. Mother and infant behaviour

Our most frequent view of mothers and their infants was when they were travelling. Infant chimpanzees were carried ventrally when small and in the dorsal position when older. This agrees with published reports, e.g., Goodall (1967). It seems likely, however, that the carrying position may depend on the circumstances. For example, an adult female was seen to approach and climb into a tree, with a large infant in the dorsal position. During the course to the observation, the chimpanzees noticed me and left quickly. This same adult female then took the infant down the tree in the ventral position and walked away with it in the ventral position. Such variation has also been seen by Goodall (1967).

On 5 occasions adult females were seen to retrieve infants. Only once was an infant seen to approach its mother before departure. Many times the initiator of the reunion could not be determined.

Goodall (1967) also described how mothers moving arm-over-arm through the trees sometimes flexed their legs to cradle a small infant. This was once seen at Mt. Assirik.

On two occasions infants took solid food from their mothers. In the first instance, the infant took handfuls of the dry flesh of the baobab fruit which its mother was eating. The infant did not beg, but simply took the food, and the mother neither helped nor hindered it. In the second example a juvenile reached out to hold the pod of the Afzelia africana which its mother was eating. After a few minutes, the mother released the pod and the juvenile took it. It is interesting to note that in these examples from Mt. Assirik, both foods were contained in hard shells that an infant could not open by itself: this was also found at Gombe (Silk, 1978).

It seems likely that at Mt. Assirik, as at Gombe (Goodall, 1975) and Budongo (Reynolds and Reynolds, 1965), siblings take an interest in their mothers' infants. Once an adult female with an infant in the ventral position was feeding in the forest with a juvenile male. The juvenile male approached the female with his hand extended, palm upwards. The infant moved off the female and into the arms of the juvenile: it then clung ventrally. The juvenile male moved through the tree without supporting the infant, but it clung sufficiently well to remain in position; then they rested on a branch. The adult female seemed unconcerned and continued to feed. Several minutes later, she approached the pair, retrieved the infant, and they all moved off together.

17. Discussion

Even from the limited description in this chapter, some interesting features of the population at Mt. Assirik emerge.

There do not seem to be any ailing chimpanzees at Mt. Assirik. The lack of signs of respiratory illness, common in great apes elsewhere, is unusual. One reason which seems likely to account for this is that chimpanzees at Mt. Assirik do not live in close proximity to human settlements and are therefore not exposed to human infections. Their wide ranging is also likely to reduce the risk of reinfection by parasites. Researchers living and working at Mt. Assirik also rarely suffered from respiratory infections, nor gastro-intestinal infections, probably for the same reasons as the chimpanzees, i.e., there was no permanent population of human beings living in the area.

There is a high proportion of mixed parties at Mt. Assirik. This is higher than that found in the other well-studied populations and probably equivalent to that found in the Kasakati Area, Tanzania,,although the evidence from that site if conflicting (Suzuki, 1969; Izawa, 1970). It seems most likely that this is influenced by the environment rather than that it is a social custom which varies across populations. It appears that two aspects of the environment interact to produce this behaviour. One is that trees are concentrated in the gallery forest. Outside these limited areas of forest, they are more scattered,in woodland and grassland. These force chimpanzees to cover large distances to exploit the food-bearing vegetation. At the same time, the same habitat supports large carnivores: lion, leopard and spotted hyena at both sites (Izawa and Itani, 1966; Ch. 3) and in addition at Mt. Assirik, the wild dog. These features distinguish the two chimpanzee habitats from the other well-documented ones. In such conditions, travelling parties of immature animals and their mothers are better protected by an adult male, even if he only serves as a deterrent, by increasing the ratio of adult to immature chimpanzees. Chimpanzees at Mt. Assirik are alarmed by the calls of lions or leopards, and Kano (1972) reported that a lion had driven chimpanzees up into trees. Thus the common occurrence of mixed parties in the savanna areas is thought to be an adaptation to wide ranging with its increased risk from predators and possibly strange chimpanzees in areas where trees are scarce. Almost all females with sexual swellings were seen in mixed parties. The exceptions were parties in which not all members could be identified, and one solitary adolescent female. This appears to differentiate Mt. Assirik from other sites where swollen females are sometimes found in sexual parties of adults only (Reynolds and Reynolds, 1965; Goodall, 1975). The finding of swollen females at Mt. Assirik almost always in mixed parties is hardly surprising, given the preponderence of this type of grouping; but it may have an effect on the mating strategies used by chimpanzees.

Among chimpanzees at Gombe, there are apparently three strategies available to adult males for mating with fully swollen (usually fertile) females. A dominant male, in the presence of other males, can maintain almost exclusive access to the swollen female merely by intimidating other males: lower-ranking males must seize the opportunity to mate when the alpha male is distracted; or else must "invite" the female to consort with them, away from all other chimpanzees (save the female's dependent offspring). Whether she follows him in order to consort, depends, to some extent, on the amount of attention, e.g., grooming or food-sharing, which he has bestowed upon her in the past (Tutin, 1978).

If at Mt. Assirik, males more frequently accompany adult females and their offspring, opportunities for giving attention to (i.e. investing in) a female and her offspring are greater. This may increase the probability that she will favour him when she next becomes receptive. Thus, as far as sexual behaviour is concerned, the importance of achieving the alpha rank is decreased and opportunistic matings in large sexual parties decrease, so that the most important strategy becomes attentiveness to females. This would be permitted by the small-sized mixed parties.

Another noticeable finding at Mt. Assirik is the low incidence of agonistic behaviours observed, compared with grooming and play. This is in spite of the fact that agonistic interactions are much more likely to be accompanied by loud vocalisations (pant-hoots and screams) and thus to attract our attention, than the other two activities. This may be an advantage of making observations from concealment. It is possible that elsewhere, human observers make chimpanzees uneasy and thus more likely to display, attack and reassure. This bias is largely removed at Mt. Assirik. A similar method was employed by Reynolds and Reynolds (1965) in the Budongo Forest, and they also saw higher numbers of grooming bouts (N = 57) and play (N = 47) than aggressive behaviour (N = 17 "quarrels"). There is no comparable basic data available for habituated chimpanzees with which to compare these two sets of results.

Chapter 8.

FEEDING

1. Introduction

This chapter is mainly concerned with the general aspects of feeding by chimpanzees. It confirms some patterns of behaviour found in other subspecies and examines some seasonal differences in the diet of chimpanzees.

Some potentially fascinating information on aspects of feeding, e.g., the balance of nutrients, sex differences in diet and behaviour, time spent feeding upon different items, and the precise amounts of food ingested could not be recorded at Mt. Assirik without habituation of the chimpanzees. This prevents an overall comparison with the study by Wrangham (1977) on *Pan. t schweinfurthii* and the detailed dietary comparisons of Hladik (1977).

There are many aspects of the feeding behaviour of chimpanzees at Mt. Assirik that *can* be described and measured. These are interesting both because little is known of feeding in the *verus* subspecies, and because of the nature of Mt. Assirik: its inter-annual variation, seasonal, climatic variation, low rainfall (see Ch..3), and its sparse vegetation (see Ch. 4).

This chapter will first discuss the methods used in the collection of data on feeding. It will then describe feeding behaviour, and finally the actual composition of the diet.

2. Methods

Data for this chapter come from three sources: direct observation of feeding behaviour, feeding remains left by chimpanzees, and faeces.

Direct observation of chimpanzees as they fed was mainly important to us a means of, a) seeing how foods were processed, and b) recording items of food which left no recognisable trace in faeces. Although we attempted to take note of all aspects of feeding, the quality of observations varied so widely that data on many points are scanty. Observations were often brief and did not permit accurate counts or the positions of feeding individuals. All observations of feeding behaviour from February 18, 1976 until May 28, 1978 were used for analysis (N = 122).

Food remains were accepted as being those of chimpanzees only under strict criteria: if they were fresh and found at a place where chimpanzees had been observed or heard immediately before; or if the method of processing involved was known to be performed by chimpanzees and not known to be performed by any other sympatric species, e.g., baobab fruits cracked by hitting against a solid surface and leaving a mark on that surface. While many likely looking remains were used as clues in searching for chimpanzees, unless they conformed to the above criteria, they are not used here.

The faeces of chimpanzees form the bulk of this chapter. More than 79 kg. of faecal matter (509 samples) were collected over the course of this study. The method is described in Chapter 4. Some other studies have used faecal analysis as a means of examining the diet of chimpanzees, but no criteria for the identification or collection have been stated, e.g., Nissen, 1931; Goodall, 1968; Suzuki, 1969. In places where baboons and chimpanzees occur together, there may have been confusion between the scats when diets were similar.

The advantages of regular faecal analysis are several: in the absence of continuous direct observation, it can yield much information on the species, and parts of species that are eaten; if all faecal samples are collected, the sampling of the diet should be random; for some foods, relative quantities of intake can be measured; it reveals important, but infrequently eaten items in the diet, e.g., meat and some insects which could be missed even with frequent direct observation (Moreno-Black, 1977). The disadvantages are few: one is that it forms an incomplete list of items in the diet, since well-digested foods form just a paste, or are so much altered as to be unrecognisable to the naked eye. Specific limitations on the data from faeces presented here are due to the methods of sampling. Without witnessing the defecation, faeces collected from the same site cannot be considered as independent samples since the same individual may have defecated twice. Thus, the samples for a given month may have come from chimpanzees which foraged independently, or one party feeding together on the same day, or even from the same individual on the same day. However, if all faeces that are found are collected, then any of these possible biases will be the same throughout the year. Finally, the number of samples varies quite widely from month to month, according to our success in finding faeces. The varying quantities of data are presented in Table 1. The data analysed for this chapter come from June, 1976, after the system had been operating for a month, until June, 1978. Some months have been excluded from the presentation because the samples were too small.

Quantification of items in the faeces is desirable as a means of estimating the proportion of the different species ingested. Suzuki (1969) also attempted to quantify items. He related directly the proportion of the bulk of faeces to the proportion ingested: this is too simple. For example, 5% bulk made up of many small fig seeds (_Ficus spp._) and 5% bulk of _Saba senegalensis_ (a large-stoned fruit) do not indicate equivalent rates of raw fruit ingested: the ratio of flesh to seed is greater in figs than it is in _Saba senegalensis_. To use residual bulk, or residual weight of items in faeces as a measure of proportional amount ingested, the ratio of every item's fresh to residual weight must be calculated. Without these ratios, one cannot quantify items in the faeces in relation to intake of fresh food. On the whole, though, the method we used was highly informative, and an improvement on earlier work: it is the lengthiest and most thorough study of chimpanzee faeces to date. The practice has revealed ways in

Table 1. The varying quality of faecal sample collection.

Year	Month	No. of faecal samples	No. of collection sites	Range of dates for data collection	Range of set sizes	Mean no. per set.
1976	JUN	51	11	1 - 30	1 - 10	4.6
	JUL	45	5	1 - 9	1 - 13	9.0
	AUG	0	-	-	-	-
	SEPT	15	2	12 - 28	1 - 14	7.5
	OCT	18	3	14 - 27	2 - 9	6.0
	NOV	20	2	12 - 25	3 - 17	10.0
	DEC	22	3	3 - 31	3 - 16	7.3
1977	JAN	28	5	2 - 9	4 - 8	5.6
	FEB	20	4	6 - 28	1 - 7	5.0
	MAR	17	4	4 - 31	1 - 10	4.2
	APR	23	8	6 - 21	1 - 6	2.9
	MAY	24	9	3 - 29	1 - 6	2.7
	JUN	3	1	3	3	3.0
	JUL	18	5	4 - 18	1 - 10	3.6
	AUG	5	2	24 - 28	2 - 3	2.5
	SEPT	7	2	20 - 21	3 - 4	3.5
	OCT	1	1	18	1	1.0
	NOV	6	1	13	6	6.0
	DEC	31	5	6 - 31	3 - 12	6.2
1978	JAN	13	5	8 - 31	1 - 4	2.6
	FEB	18	4	22 - 24	1 - 8	4.5
	MAR	20	4	3 - 21	4 - 6	5.0
	APR	32	7	13 - 30	1 - 15	4.6
	MAY	45	9	1 - 28	2 - 16	5.0
	JUN	27	3	14 - 18	7 - 13	9.0
TOTAL		509	105	-	1 - 17	5.1

which the method could be made even more successful.

3. Feeding Behaviour

3(i) Diurnal Variation

Chimpanzees at Mt. Assirik were observed feeding during every daylight hour, from 0600 - 1900 hours. The number of hours during which all or part of an observation took place was 141; the number of separate observations of separate food items being eaten was 122. Most observations took place between 1000 and 1200 hours (N = 39, 27%), see Figure 1.

Figure 1 shows a depression in observations of feeding over the hours 1300 - 1500. A similar depression was found by Wrangham (1977) for eastern chimpanzees. At Mt. Assirik, however, results are from chance encounters with numerous individuals, and not from continuous observations of single individuals. Due to the high afternoon temperatures, observers tended to stay in camp during the early hours of the afternoon. Thus, lack of observation of feeding by chimpanzees at Mt. Assirik at this time may be due to lack of searching: this is supported by the lack of a corresponding peak in either travelling, or resting and grooming (see Fig. 1). To see if changes of frequency in observed behaviours over the course of the day were a result of variation in observers' daily activity, the three types of behaviour were tested for correlation with one another, for both morning and afternoon periods. None were significantly correlated (Kendall Rank Correlation Coefficient, $\alpha = 0.05$). Within each type of behaviour, no significant differences were found for any hours of the day (Kolmogorov-Smirnov One-sample test, $\alpha = 0.05$). This means that although observational biases cannot be ruled out, they did not exert an obvious distorting effect.

The peaks in feeding behaviour do not correspond by the hour with those of either Goodall (1968) or Wrangham (1977), but given the comparatively small sample sizes for Mt. Assirik, and the disagreement between the two sets of data from Gombe, this is not surprising. Different sampling methods were used in each case. At Mt. Assirik there appear to be three peaks

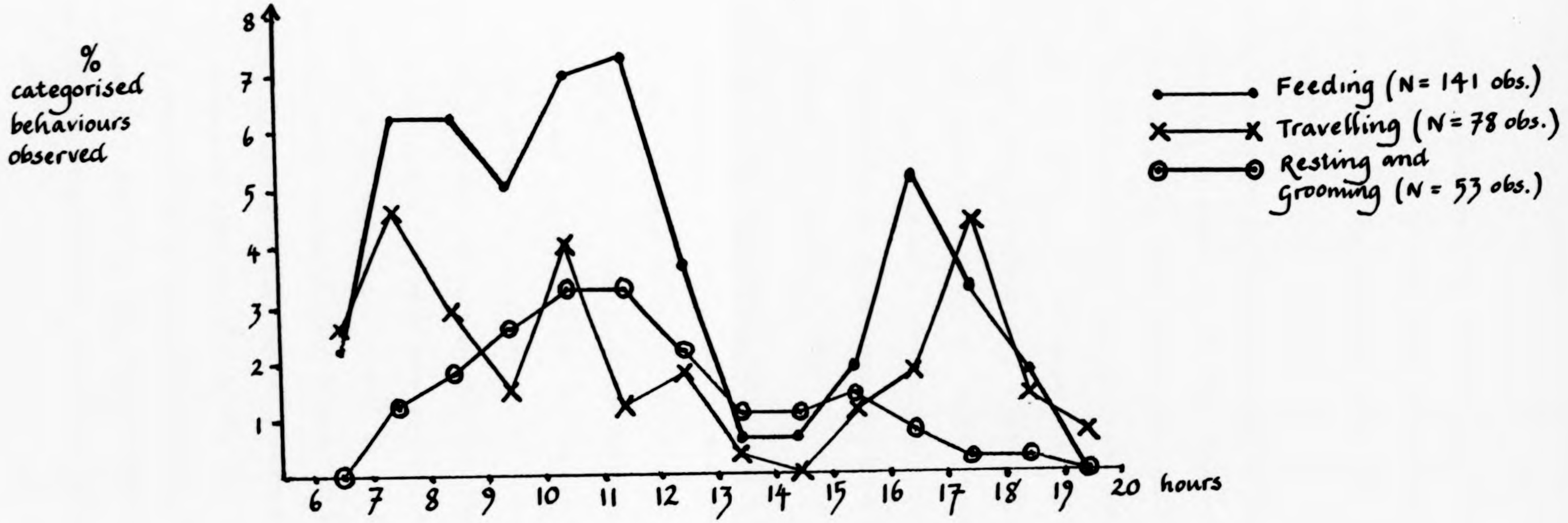


Figure 1. Diurnal variation in observations of feeding, travelling, and resting and grooming.

during the day: Wrangham (1977) also found three, although not at the same hours. It seems likely that there is a reduction in active feeding during the early hours of the afternoon at Mt. Assirik, but the data cannot confirm it statistically.

Both the other subspecies, Pan t. troglodytes (Hladik, 1977) and Pan t. schweinfurthii (Wrangham, 1977) have shown diurnal rhythms in the eating of fruits and leaves, with fruits being eaten most frequently in the morning. Unfortunately, observations of chimpanzees eating leaves at Mt. Assirik (N = 6) are too few for comparison. Hladik (1977) found seasonal variation in this rhythm of food choice which he related to the abundance of the different food types. As Mt. Assirik is a highly seasonal habitat, there may well prove to be a similar variation in diurnal rhythm, with flushing leaves being eaten throughout the day at the end of the dry season, when they are most common.

3 (ii) Feeding Position Relative to the Ground

In 88% (N = 106) of observations of feeding where position could be determined, chimpanzees were in trees. In only 12% (N = 14) of cases did they feed on the ground. In two cases the position could not be ascertained. Wrangham (1977) found that chimpanzees at Gombe spent 88% of time feeding in trees in the wet season, but as little as 57% during a dry season. He attributed this difference to more ground-level plant production and a preference for the fallen fruits of some species, e.g., Parinari curitellifolia, in the dry season, as well as the chimpanzees' dislike of sitting on damp ground during the wet season. At Mt. Assirik there was no significant difference in this behaviour between wet and dry seasons (X^2 for two independent samples: $X^2 = 0.188$, df = 1, $p > 0.8$). The high percentage of observations of chimpanzees feeding in trees at Mt. Assirik may be inflated by their being more visible there than on the ground. Being unhabituated, they are more easily seen from a distance when in the trees.

4. Feeding Techniques

4 (i) Fruit

Chimpanzees ate fruit (i.e., the pericarp) with varying speed and intensity from idle picking, slow inspection, sucking and chewing, to stuffing the mouth without inspection and swallowing them quickly. They were sometimes seen to test figs by squeezing the fruits between thumb and forefinger. They were also seen on some occasions to protrude the lower lip and look down at the food contained within. This has been noted by Goodall (1968).

Some fruits required special processing. Baobab fruits, when fully ripe, have large woody shells (i.e., the outer pericarp) about the size of rugby balls (see Fig. 2) and chimpanzees were seen and heard to crack these open. The method was to hold the end of the long stem in one hand and swing the fruit repeatedly, so that it hit the branch or trunk of the tree at a rate of about 1 swing/second. The mean number of blows was 16 (range = 3 - 56 N = 22 series). Soft fruits with large stones, e.g., _Spondias mombin_, were often chewed and swallowed whole, but the largest stones, e.g., _Cola cordifolia_, which has a stone the size of a brazil nut with shell, were sometimes spat out. Small fruits, e.g., _Ficus ingens_, or fruits with much fibrous flesh and many small seeds, e.g., _Oncoba spinosa_, were sometimes found spat out in mouth-sized quids which had apparently been well-sucked and chewed. This has been reported before for western (Nissen, 1931),eastern (Goodall, 1968) and central African chimpanzees.(Hladik, 1977).

Fruits were eaten both directly from the twig or after being picked by hand. Tough skins were torn open with the incisors and the flesh from inside pulled out by teeth and fingers.

4 (ii) Leaves

Chimpanzees were rarely seen eating leaves (N = 6 observations). Leaves from trees and bushes were plucked off both with the lips and by hand, prior to being chewed.

Figure 2. Fruits of the baobab.

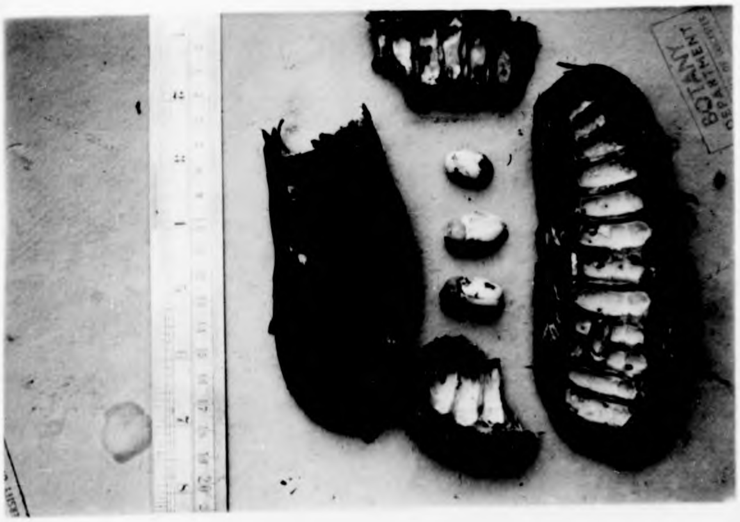


Figure 3. The pods of Afzelia africana.

4 (iii) Seeds

In almost all cases of seed-eating, the seeds were contained in pods which were soft and easily opened. The lining of the pod was also removed and eaten in some cases. There were two exceptions to these easily opened pods: one was with the seeds of the baobab fruit, mentioned earlier, the other was *Afzelia africana*. The seeds of the latter species are contained in large, broad, flat, woody pods (see Fig. 3): the pods are hard, even when unripe. When chimpanzees first begin to eat the seeds, the pods are difficult to open but are cracked across the seam with the teeth and torn open with both the teeth and hands. Later, the pods harden and become virtually impossible to open. Finally, several months later, the pods dehisc, making the seeds easily available. Difficulty in the processing of this pod is the most likely factor causing the two peaks of highest frequency of this item in the diet over the course of the year (see section on seasonal variation in diet).

When fully mature, the seeds themselves were hard and unless thoroughly chewed, passed through the digestive system unchanged. Baobab seeds, although soft inside, developed tough testa and they could also pass through the chimpanzee's alimentary tract without being digested.

4 (iv) Flowers

Flowers and flower buds were seen to be eaten whole on 4 occasions. The only other observation of flower-eating occurred when two adolescent chimpanzees were seen in a very delicate feeding operation. They were feeding in the Red Silk Cotton tree (*Bombax costatum*) which has a spiny trunk and branches. The chimpanzees entered the tree by way of an adjacent one, and gingerly stepped through the tree, slowly reaching for the large red flowers. They held each flower cupped in one hand, and, balancing with the other hand, they carefully ate the stamens from the centre.

4 (v) Stems

The only stems identified by species as food for chimpanzees were those of bamboo (Oxytenanthera abyssinica). Feeding remains revealed that stems of the current year's growth were snapped off and sections chewed and sucked, then spat out when most of the moisture had been withdrawn. This is the manner described by Suzuki (1969) for eastern chimpanzees eating bamboo, and by Jones and Sabater Pi (1971) for feeding on stems by the central subspecies.

4 (vi) Bark

Chimpanzees were never seen to eat bark. Fresh remains of bark were found after observation of chimpanzees, however. By teeth marks (see Fig. 4),it appeared as if they had torn off strips of bark with the teeth and scraped off the inner cambium layer with the incisors, in the manner described by Goodall (1968) for Gombe, and by Nishida (1976) for Kasoge.

4 (vii) Honey

Although honey is eaten often (see section on diet) it was only once seen being collected. An adult female chimpanzee walked,carrying a 15 cm. diameter section of honeycomb in her mouth. It seems that chimpanzees at Mt. Assirik merely break off sections of honeycomb. The bees producing this honey are arboreal or cliff-dwelling, rather than subterranean. No evidence has emerged of the use of tools to obtain honey, as was found by Merfield and Miller (1957) or A. Goodall (1979) for underground bees' nests, and Izawa and Itani (1966) for an arboreal nest.

4 (viii) Insects

The use of tools to obtain insects has been reported from several studies: for termites, Goodall (1963), Suzuki (1966) and Jones and Sabater Pi (1969); for driver ants, Goodall (1968); for several species of arboreal ants, Nishida (1972) and Hladik (1973).

Insects are important as food for the chimpanzees at Mt. Assirik, as will

Figure 4. Feeding remains of bark.

be shown, but the only insects seen to be gathered were weaver ants (Oecophylla longinoda). An adult female chimpanzee climbed a small Combretum tree and detached a weaver ant nest. This she rubbed quickly between her palms, crushing it, presumably to kill the ants inside. She then descended, and carrying the nest in one hand, took it under a shady bush, out of view. Remains of leaves from the nest were found there later. The method is similar to that employed by chimpanzees at Gombe (Goodall, 1968).

Army ants (Megaponera foetens) are eaten. Their remains are found in faeces, but we do not know the technique employed to obtain them. They have a severe sting and are not known to be eaten at Gombe, although present there (McGrew, pers. comm.).

Driver ants (Dorylus (Anomma) nigricans) are also found in faeces and we have strong circumstantial evidence for the technique used to obtain them. On one occasion when we had heard chimpanzees calling the evening before, we set out in the morning to search the appropriate area. We came across a mass of driver ants among the roots of a tree. Almost all of them were reared up in the defensive posture. Five sticks, stripped of leaves, protruded vertically from holes among the tree roots. A further 4 sticks lay on the ground, all stripped of leaves. Another stick had been partially stripped. Freshly torn leaves lay strewn about.

The circumstantial evidence of the modiciation of sticks is a necessary part of their qualification as tools (McGrew et al., 1979). We pulled out the erect sticks to find masses of ants biting onto the distal ends. It appeared that we had disturbed chimpanzees in the process of "dipping" for ants (McGrew, 1974). The tools are shown in Figure 5. The lengths range from 36 - 161 cm., with a mean of 71.6 cm. Most of the tools came from a Garcinia ovalifolia tree growing only 3 metres away. One tool, the longest, was made of a vine, and one was a dead stick, which could not be identified. Some of the tools were frayed from repeated usage, and 2 had broken off fragments, see Figure 5.

Figure 5. Ant-dipping tools.

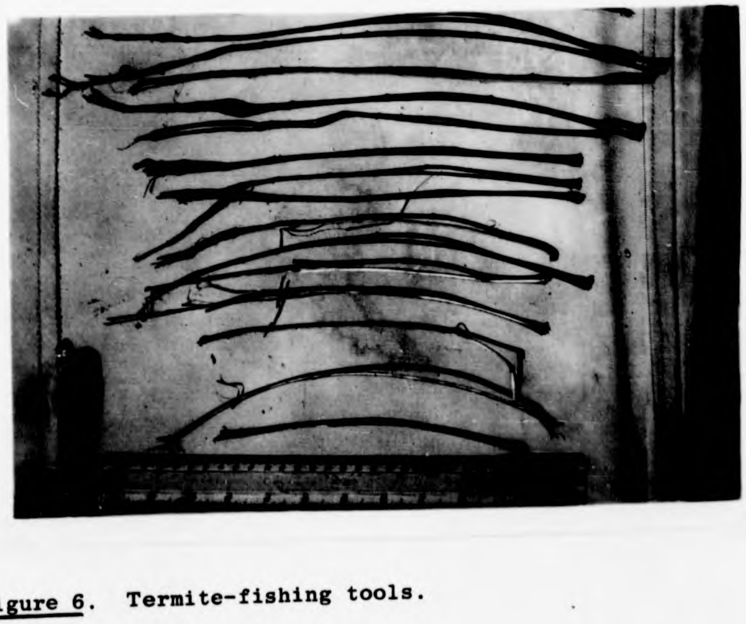


Figure 6. Termite-fishing tools.

These lengths are similar to those reported from Gombe. Goodall (1968) recorded tools as usually between 45 - 75 cm., but one was 100 cm. long. McGrew (1974) measured 13 tools and found a mean length of 66 cm. (range = 15 - 113 cm): he also noted that tools were stripped of leaves. In addition to these two reports from Gombe, Nishida also reported the use of tools by the eastern subspecies to obtain ants, and Hladik (1973) reported the use of tools to obtain ants among the central subspecies. The data presented here provides the first evidence of the use of tools by Pan t. verus to obtain ants.

Termites (Macrotermes subhyalinus) are found seasonally in the faeces of chimpanzees, and again there is convincing evidence of tools having been used to obtain them. Over the course of two years, we collected tools from 13 different termite mounds at Mt. Assirik (see Fig. 6). These tools were found lying on and around the mounds. Only 1 of 173 tools was found implanted in a mound; this happended after observers watched a chimpanzee sitting huddled by a mound, with its back to them. The chimpanzee departed. The observers approached the mound and found this tool, along with others scattered around the mound. On another occasion, observers followed the trail of vocalising chimpanzees, and this led to a termite mound covered with fresh tools.

Of the 173 tools measured, the mean length was 32.5 (range = 13 - 71 cm). These are similar lengths to those found at Gombe (N = 145) where mean length was 30.7 cm (range = 7 - 100 cm), but different from tools found to have been used by Pan t. troglodytes in Rio Muni for obtaining termites (Sabater Pi, 1974). A full discussion of similarities and differences across these populations and the implications of the findings is given in McGrew et al. (1979). Most tools at Mt. Assirk were made from twigs (47%) and leaf stalks (31%): only 19% were made from vines and 3% from grass. As it will be shown later for the appearance of termites in faeces, tools are found seasonally. Over the course of three years it was found that 89% of tools were found during the month of June, at the beginning of the rainy season.

The use of tools to obtain termites has been reported in the eastern chimpanzee (Goodall, 1965; Suzuki, 1966), the central subspecies (Jones and Sabater Pi, 1969) and was recently reported for this population (McGrew et al., 1979). These results invalidate statements made by Struhsaker and Hunkeler (1971) and others that fishing for termites is restricted to areas east of the Dahomey Gap.

The number of tools (N = 173) found beside 22 termite mounds was much greater than those found on the one occasion beside the occupied driver ant nest (N = 10). Nevertheless, the ant-dipping tools proved to be significantly longer (Median test: $X^2 = 14.28$, $p < 0.001$, N = 183). Thus the manufacture of the two types of tool, and probably the techniques used to gather the insects are thought to differ. This was noted in the Gombe population and emphasised by McGrew (1974).

4 (ix) Meat

Although the remains of mammals were found in the faeces of chimpanzees, we never observed the capture or consumption of prey. The species of prey, however, indicate likely techniques used to obtain them. All the positively identified remains have been of nocturnal prosimians. These are inactive during the day, asleep in tree hollows or cryptic nests. Presumably they are eaten opportunistically when chimpanzees happen to come across a nest. The prey have little chance of escape. Thus chimpanzees do not need to expend much energy in hunting, unlike cases reported from populations of eastern chimpanzees where species of prey are diverse and include diurnally active monkeys (Suzuki, 1975; Wrangham, 1975; Nishida, 1979). Only one case of chimpanzees preying upon nocturnal prosimians has been reported before: this report came from Kasoge, Tanzania (Nishida, 1979).

It may be that chimpanzees at Mt. Assirik eat only these diurnally inactive prey. There is no evidence of their eating green monkeys, (Cercopithecus aethiops), or the young of bushbuck (Tragelaphus scriptus) which occur at Mt. Assirik (see Ch. 3) and which are eaten elsewhere (Wrangham, 1975;

Nishida, 1979). The apparent specialisation in nocturnal prosimians indicates a different technique of acquisition of prey from that which has been seen in East Africa. Catching bush babies or pottos by day is presumably carried out by individuals foraging opportunistically, or chancing upon them, with little likelihood of cooperation from others. (The question of whether chimpanzees hunt cooperatively at Gombe is debatable (Teleki, 1973; 1975; Busse, 1978). It may also be as likely for a female to find and eat them as a male. The observation of an adult female in the rehabilitation project eating two bush babies (McGrew *et al*. 1978) supports this. This could represent another difference between the chimpanzees at Mt. Assirik and the only other carnivorous population for which detailed, long-term data are available: at Gombe, males capture prey more often than females (McGrew, 1979).

5. Carrying food

Over the course of this study, 10 chimpanzees were seen carrying food. It was carried by hand 3 times as the chimpanzees walked tripedally. It was carried by mouth 8 times. On one occasion, an adult male carried a huge fruit (*Treculia africana*) weighing 3.5 kg. in his mouth for a distance of 210 metres (see Fig. 7). Branches bearing fruits, single fruits, leaves, and a section of honeycomb were all seen to be carried. Carried food has been seen in a provisioned population of *Pan t. verus* (Albrecht and Dunnett, 1971), and the dragging away of branches of fruit was reported by Nissen (1931), also for the western subspecies. Reynolds and Reynolds (1965) reported the carrying of food in *Pan t. schweinfurthii*.

6. Reingestion of items in faeces

Coprophagy among captive chimpanzees has been considered to be an unnatural habit as a result of confinement (Morris, 1964). Circumstantial evidence from Mt. Assirik, however, suggests that wild chimpanzees pay attention to faeces as a potential source of food. Once a party of chimpanzees rested

Figure 7. The fruit of Treculia africana, which was carried by a chimpanzee.

Figure 8. The limb of a bush baby, which was recovered from chimpanzee faeces.

in trees; other chimpanzees were on the ground, but could not be seen well. After half an hour, they saw us and left. We approached the resting site and found fresh faeces spread out on a rock; all the baobab seeds were moved to one side. Many of these had been opened (after defecation) and the kernels extracted. On a second occasion after observing chimpanzees, we approached the site of the observation and found fresh faeces spread about and apparently picked through. The faeces contained large pieces of meat, one of which may be seen in Figure 8. The limb was almost undigested.

From these examples, and one given by Wrangham (1975) of meat being reingested from faeces, it seems that in the wild, chimpanzees will extract certain items from faeces, presumably if the food is high in energy. Babobab kernels are high in protein and lipids (Kerharo and Adam, 1974) and meat is a concentrated source of protein. Chimpanzees feed mainly on vegetable food low in protein (Hladik, 1977) and must therefore consume large quantities of bulk quickly in order to obtain sufficient protein. Such digestion is suitable for foods which can be easily broken down, but seems inadequate for tough-skinned seeds such as baobab or meat, that have not been thoroughly chewed. These foods may pass through the chimpanzee, and the energy spent gathering them as well as the calories and nutrients in the food may be wasted, unless they are reingested. It seems that the digestive system is adapted for the bulk of the diet, and that reingestion of high protein foods from faeces is an adaptation to overcome the occasional wastage that such a digestive system entails.

7. Drinking

Chimpanzees were observed drinking four times. Twice the water was running; on the other two occasions it was still. In each case, the chimpanzee crouched down and sucked water directly with the mouth. This is the same action as that described by Nissen (1931) and Goodall (1968). Reynolds and Reynolds (1965) also report a chimpanzee dipping its hand into water in a tree-hole and licking the water off its fingers. Similarly, Hladik (1973) saw reintroduced chimpanzees obtaining water from tree-holes by dipping in the hand, then letting the water drip from the hand into the open mouth. We found no evidence of leaves having been made into sponges, by crumpling, in order to obtain water in tree-holes, as described by Goodall (1968) and Hladik (1973).

It is not known how often chimpanzees need to drink water at Mt. Assirik. Human beings, after acclimatisation, and when out in the field, need to drink about 6 litres of water per day in the dry season. No comparative rates of drinking are available for chimpanzees elsewhere, although Hladik (1973) states that in the dry season in Gabon, it is at least once a day. This indicates little, however, about how long chimpanzees can go without water, if obtaining it requires an inconvenient detour, as must often be the case at Mt. Assirik.

Chimpanzees were heard to give excited pant-hoot calls on arriving at the head of the gallery forest of Lion Valley, where water begins. Whether the excitement was due to the proximity of shade, food, or possibly water, one cannot say.

8. Diet

8 (i) General Composition

From direct observation and faecal evidence, it is clear the the chimpanzees at Mt. Assirik are omnivorous: they eat fruit, seeds, stems, flowers, leaves, bark, honey, assorted insects and meat. The bulk of their diet (60% of items) consists of fruits. The predominance of fruit in the diet has been found throughout the range of chimpanzees (Nissen, 1931; Azuma and Toyoshima, 1962; Goodall, 1963; Reynolds and Reynolds, 1965; Jones and Sabater Pi, 1971).

A complete list of vegetable foods and other items may be seen in Table 2, along with the type of evidence for them. It can be seen that most evidence comes from faecal contents. This is worth noting since most

Table 2. Items in the diet and the type of evidence for them.

Family	Species	Fruit	Whole seed	Crushed seed	Pod lining	Leaves	Flowers	Stem Bark	TYPE OF EVIDENCE		
									Direct obs.	Faecal remains	Confirmed remains
ANACARDIACEAE	*Lannea acida*	X	X						X	X	X
	Lannea microcarpa	X	X						X	X	X
	Pseudospondias microcarpa	X	X						X	X	X
	Spondias mombin	X	X						X	X	X
ANNONACEAE	*Annona senegalensis*		X							X	
	Hexolobus monopetalus	X	X						X	X	X
				X						X	
						X			X		X
APOCYNACEAE	*Landolphia heudelotii*	X	X						X	X	X
	Saba senegalensis	X	X						X	X	X
BOMBACACEAE	*Adansonia digitata*	X	X						X	X	X
				X						X	X
							X				X
	Bombax costatum						X		X		X
	Ceiba pentandra			X						X	
						X			X		X
BORAGINACEAE	*Cordia myxa*		X							X	
CAESALPINIACEAE	*Afzelia africana*		X	X					X	X	X
	Cordyla pinnata	X									X
	Diospyros mespiliformis	X	X						X	X	X

Table 2 contd.

										TYPE OF EVIDENCE		
Family	Species	Fruit	Whole seed	Crushed seed	Pod lining	Leaves	Flowers	Stem	Bark	Direct obs.	Faecal remains	Confirmed remains
	Piliostigma thonnningii			X							X	X
					X						X	X
	Tamarindus indica		X	X							X	
					X						X	
COMBRETACEAE	*Combretum tomentosum*			X						X	X	X
FABACEAE	*Pterocarpus erinaceus*					X				X		
							X			X	X	X
									X			X
FLACOURTIACEAE	*Oncoba spinosa*	X	X								X	X
GUTTIFERACEAE	*Garcinia ovalifolia*	X	X								X	
ICACINACEAE	*Icacina senegalensis*		X								X	
LOGANIACEAE	*Strychnos spinosa*	X	X								X	
MENISPERMACEAE	*Parkia biglobosa*			X						X	X	X
					X					X	X	X
							X			X	X	X
MOROCEAE	*Ficus ingens*	X	X							X		X
	Ficus umbellata	X	X							X	X	X
	Ficus vallis-choudae	X	X							X		X
	Treculia africana	X	X							X	X	X
POACEAE	*Oxytenanthera abyssinica*							X			X	X
RHAMNACEAE	*Zizyphus mucronata* ?		X								X	

Table 2 contd.

											TYPE OF EVIDENCE	
Family	Species	Fruit	Whole seed	Crushed seed	Pod lining	Leaves	Flowers	Stem	Bark	Direct obs.	Faecal remains	Confirmed remains
	Zizyphus spina-christi?		X								X	
RUBIACEAE	*Nauclea latifolia*		X								X	
SAPOTACEAE	indet.		X								X	
SIMARUBACEAE	*Hannoa undulata*	X	X								X	X
STERCULIACEAE	*Cola cordifolia*	X	X							X	X	X
TILIACEAE	*Grewia lasiodiscus*		X								X	
						X				X		X
VERBENACEAE	*Vitex madiensis*		X								X	
VITACEAE	*Cissus populnea*	X	X								X	X
Unknown	Unknown (109)		X								X	
	Unidentified seeds		3								X	
	Unidentified grasses							X			X	
	Unidentified shoots							X			X	
TOTALS	44	20	34	8	3	4	4	3	1	25	44	34

Table 2 contd.

Food Type	TYPE OF EVIDENCE Direct obs.	 Faecal remains	 Confirmed remains
INSECTS			
Dorylus (Anomma) nigricans		X	
Oecophylla longinoda	X	X	X
Macrotermes subhyalinus		X	
Megaponera foetens		X	
Apis mellifera		X	
Honey (Wax)	X	X	
MAMMALS			
Galago senegalensis		X	
Perodicticus potto		X	

studies tend to rely on feeding remnants. Not only is this risky, since they may not be confirmed as those of chimpanzees, but they are not as informative as faecal analysis. Only 2 items of food were confirmed from feeding remains and not by any other source; and only 2 items were confirmed by direct observation and not by any other source; but 17 types of food were identified only by means of faecal analysis. This further emphasises the value of the technique in studying an unhabituated group of chimpanzees.

In Table 2, fruits and their whole seeds are put together since whole seeds are presumed to be swallowed during the course of eating the flesh of the fruit, and not purposefully. Crushed seeds are listed separately, since it is thought that these are crushed to make the contents digestible: these form 15% of items in the diet. Identification of species of leaves, stems, and *Ficus* and *Lannea* fruits depends upon direct observation. Data by this method are scarcer than faecal data, so the number of species of leaves and stems eaten is likely to be greater than those listed. Similarly it is likely that chimpanzees eat two further species of *Ficus* and one of *Lannea*, but this cannot be confirmed.

A minimum of 56 different vegetable foods, i.e., parts and species including the general categories of unidentified seeds, grasses and shoots, have been confirmed. This exceeds the number reported by Reynolds and Reynolds (1965) and Sabater Pi (1978), but much fewer than those reported for chimpanzees in Tanzania by Suzuki (1969), Nishida (1974) and Wrangham (1977). It is tiny compared with the 285 vegetable foods eaten by chimpanzees re-introduced in Gabon (Hladik, 1977). Table 3 shows a comparison of these records. The number of different foods does not seem to be associated with length of study, gross habitat type, or methods. Although Mt. Assirik might be expected to have fewer vegetable foods to offer because of its sparse vegetation, it is likely that some foods that are eaten infrequently, and which do not leave macroscopic traces in the faeces, are missing from this list.

Table 3. A comparison of the number of parts of species recorded as chimpanzee foods from 7 different sites.

Site	Budongo Forest	Rio Muni	Mt. Assirik	Kasakati Basin	Gombe	Kasoge	Gabon
No. of species and parts	40	51	56	78	201	205	285
Type of habitat	Forest	Forest	Savanna	Savanna	Mosaic	Mosaic	Forest
Length of study (months)	8	17	28	16	180	84	12
Report	Reynolds & Reynolds (1965)	Sabater Pi (1978)	This study	Suzuki (1969)	Wrangham (1977)	Nishida (1974)	Hladik (1977)

At least five species of insect are consumed at Mt. Assirik: termites (Macrotermes subhyalinus), weaver ants (Oecophylla longinoda), driver ants (Dorylus (Anomma) nigricans), army ants (Megaponera foetens) and bees (Apis mellifera). Bees fall into a separate category, since, although they are found in faeces, they may be crushed and swallowed unintentionally in the course of eating honey (bees' wax is also commonly found in faeces). The common occurrence of the bees in the faeces, however, indicates that they may provide an important contribution to the food intake of chimpanzees. A single wasp was once found in a faecal sample. More species of insects are eaten in Tanzania (Goodall, 1968; Suzuki, 1969) and in Gabon (Hladik, 1977).

Honey is eaten frequently at Mt. Assirik as evidenced by the common occurrence of bees (23% of all samples) and bees' wax (18% of all samples) in faeces. Items that appeared to be pupal cases were also found occasionally. Honey is also known to be eaten by eastern chimpanzees (Izawa and Itani, 1966; Goodall, 1968) and the central subspecies (Merfield and Miller, 1957).

Analysis of the faecal samples revealed that chimpanzees at Mt. Assirik eat meat. Eastern chimpanzees are known to eat mammals (Goodall, 1963; Teleki, 1973; Izawa and Itani, 1966; Kawabe, 1966; Suzuki, 1971; Nishida, 1979). From June 1976 to June 1978, 7 out of 509 faecal samples contained the remains of mammals. This gives a percentage of 1.4: this is lower than the published rate of 2.6% (McGrew et al., 1979). This is due to the analysis for this chapter having been carried out on a more recent block of data. With such low frequencies, the samples chosen for analysis are likely to alter the percentage rates. Even the figure of 1.4% shows that by comparison with other carnivorous populations where faecal analysis has been carried out, Mt. Assirik has a higher percentage than the Kasakati Basin (Suzuki, 1966) but lower than Gombe (Goodall, 1968). These results argue against criticisms made of the results from Gombe, where chimpanzees are provisioned, that meat-eating among chimpanzees is an artificial habit

(Gaulin and Kurland, 1975; De Pelham and Burton, 1976) induced by the provisioning of bananas. Although the rates may have been inflated as a result of provisioning as Wrangham (1974) and Reynolds (1975) suggested, these results from a truly wild population of chimpanzees demonstrate that it is a natural element in the diet (McGrew *et al*., 1979).

The mammalian remains found in faeces were identified: 2 samples contained remains of bush babies *(Galago s. senegalensis)*: 3 contained remains of *Galago* but the species, either *senegalensis* or *demidovii* could not be determined. It is more probably *senegalensis*, since *demidovii* has not been recorded in the park (Dupuy, 1971). Two samples contained remains of a potto (*Perodicticus potto*). This is considered a forest species and has not been recorded within the park (Dupuy, 1971). Presumably, it inhabits the small areas of gallery forest. Other remains have not been identified.

There was an extraordinary finding of 2 pieces of sloughed snake skin (each about 10 x 20 cm) in one faecal sample. These were later identified as coming from a cobra (either *Naja haje* or *N. nigricollis)* at least 2 m long.

8 (ii) Seasonal variation in fruit and leaves

In order to examine seasonal variation, i.e. the extent to which the frequency of a food item fluctuates over the course of a year, the method of calculating seasonal indices from faecal analyses of the sloth bear (*Melursus ursinus*), used by Laurie and Seidensticker (1977, p.195), was considered. The formula gave some confusing results for the present data. It showed monthly differences well, but where a fruiting season stretched over several months, the results gave a low index, even when the incidence within those months was high. For example, by this method, at Mt. Assirik the fruit of *Saba senegalensis* (see Fig. 9) found in 40% of faeces had a seasonality index of 11.4. Compare this with chimpanzee hairs found in faeces, which rarely occurs (2% of faeces): these have a seasonality index of 31.7. The index is really one of monthly differences and concentrates

Figure 9. Most commonly eaten foods, June - Dec. 1976: the dotted line indicates insufficient data.

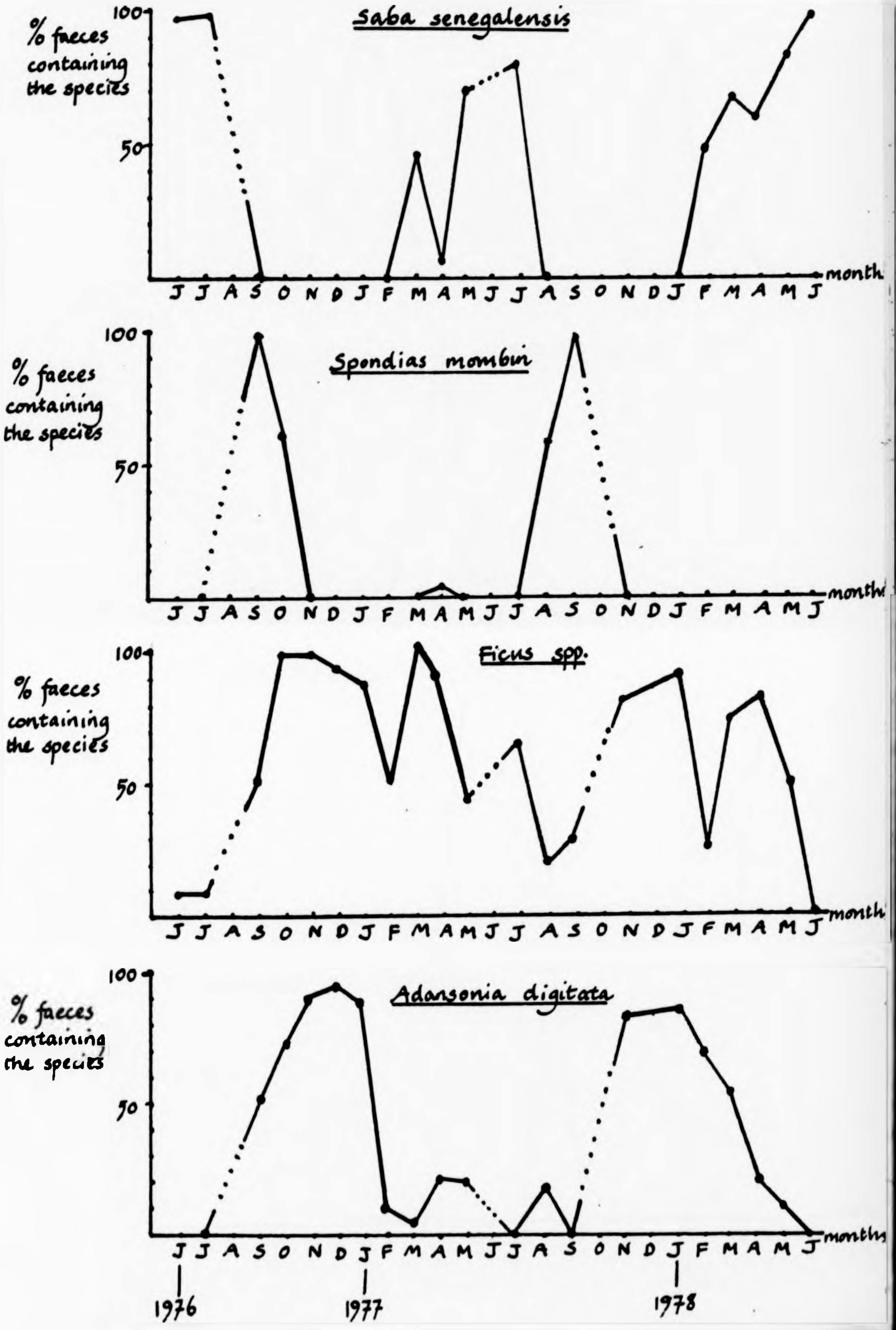


Figure 10. Most commonly eaten foods Jan. - Aug. 1977, excluding *Ficus* (March) and *Saba* (July), which appear in Figure 9.

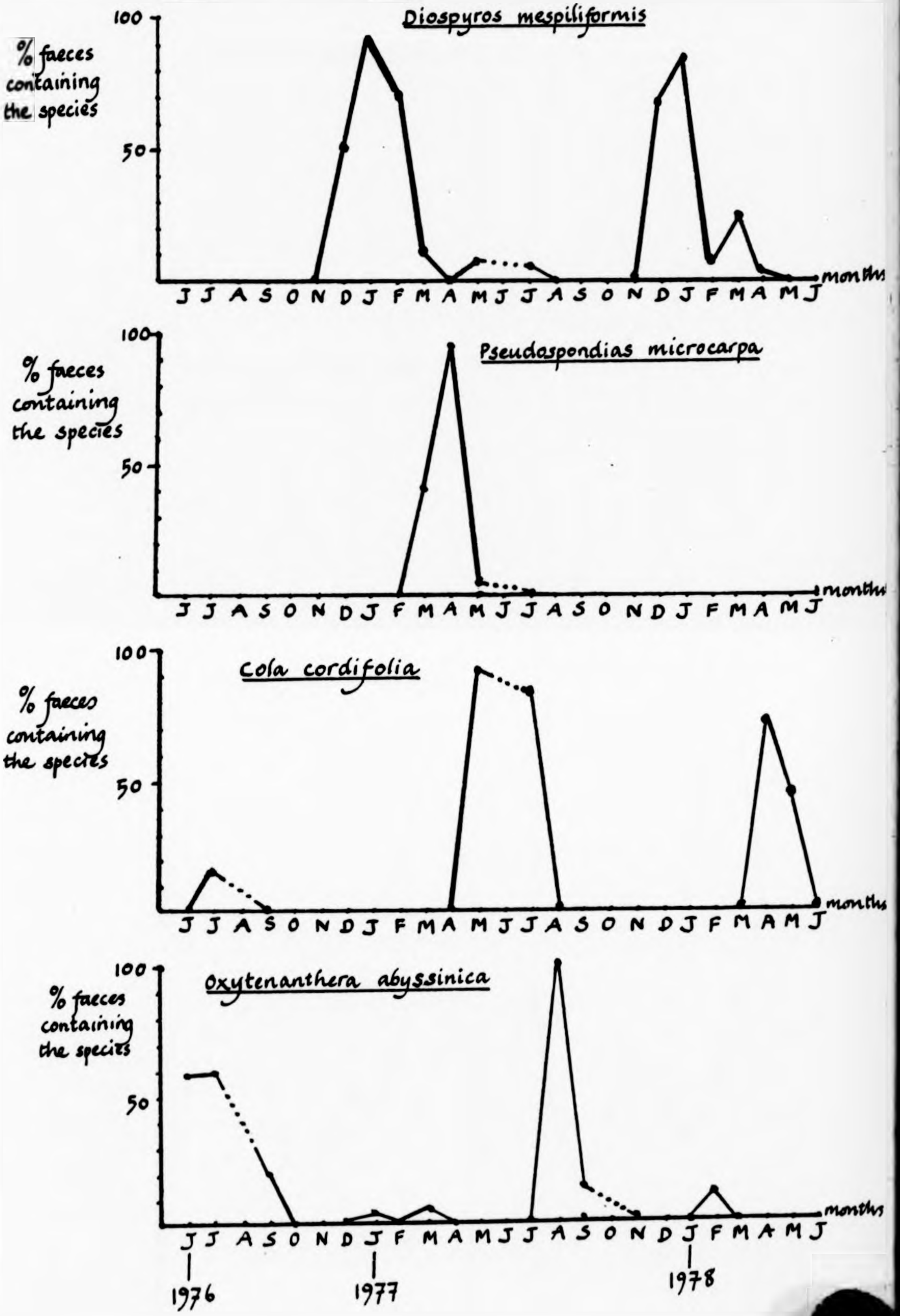
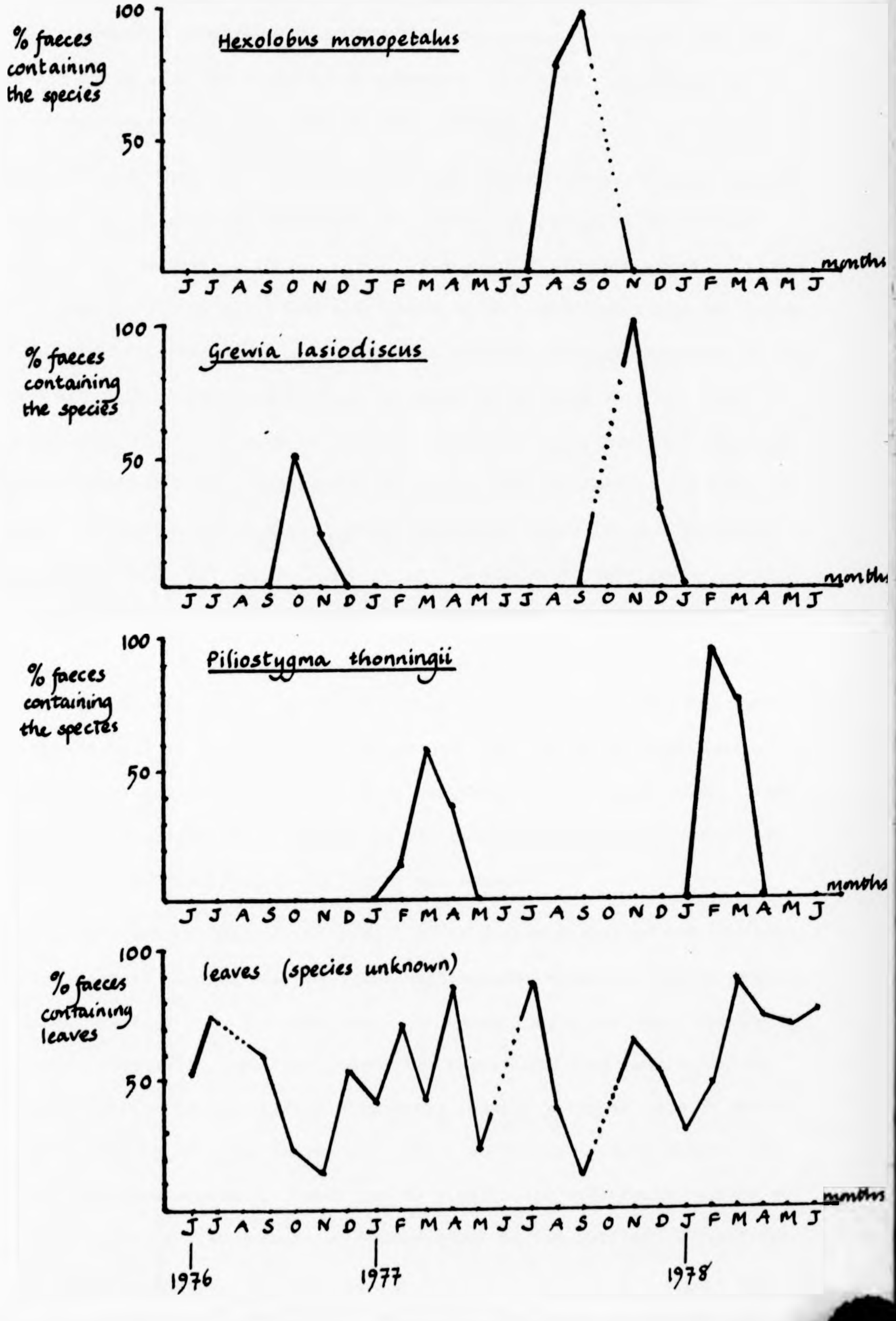


Figure 11. Most commonly eaten foods, Sept. 1977 - June 1978 excluding *Spondias* (sept.), *Ficus* (Dec., Jan., April), and *Saba* (May, June), which appear in Figure 8.



on the month of highest frequency, ignoring other months of high frequency. It cannot distinguish between low frequencies occurring sporadically, and high frequencies clustered over more than one month. It may be suitable for the diets of other species but cannot be used here. A formula for a comprehensive seasonality index is sadly lacking.

In a further attempt to look at the seasonality of foods, allowing for the varying size of samples per month, the foods were ranked by percentage frequency of appearance in the faeces, per month. All foods ranked first in frequency for any month are considered to be staple foods and are shown on the graphs in Figures 9 - 11. Slashed bars below graphs indicate months which had to be eliminated because of insufficient data ($N < 5$). The figures show, by the series of peaks of high frequency, how each important food succeeds the last, throughout the year. Most foods have one peak per annum. Exceptions are Pseudospondias microcarpa (Fig. 10) and Hexolobus monopetalus (Fig. 11) which failed to have peaks in certain years and will be discussed as examples of inter-annual variation. Other exceptions are Ficus spp. (Fig. 9) and miscellaneous leaves (Fig. 11). As the graph shows, several species of Ficus are important fruits throughout the year. The depressions in the graph may be because other foods are sometimes preferred, or because no species of fig happens to be fruiting then. Each species could not be distinguished in the faeces, and thus one cannot say whether or not each species had a discreet season.

Leaves are eaten throughout the year: 55% of faeces contained the remains of some leaves. Again, one could not distinguish between different species in faecal remains with the naked eye. It seems likely that many species are eaten seasonally, when the leaves are young, and have less cellulose (Hladik, 1977). Of the samples containing leaves, analysis of each sample revealed that in 48%, few leaves occurred, in 37% leaves were common, and in 15% they were abundant. There was no significant difference between wet and dry seasons in the amounts of leaves found in the samples (X^2 test for two indpendent samples; $X^2 = 5.12$, $df = 2$, $0.1 < p < 0.5$, $N = 299$). The results suggest a trend, however, with leaves tending to be eaten in greater quantities in the dry season.

These graphs also indicate the varying lengths of vegetable food seasons. Saba senegalensis and Adansonia digitata are eaten at various stages of development (Fig. 9): Grewia lasiodiscus and Piliostygma thonningii (Fig. 11) have short seasons.

An unusual example of seasonality in one species of food is that of Afzelia africana. This has two seasons per annum (see Fig. 12). As mentioned in the section on techniques, there is a time in the development of the seed case (around September), when it can be opened with the teeth and the seeds extracted. Then the pod apparently becomes too tough and woody to open. By February, the pods have dehisced, allowing the chimpanzees to obtain the seeds easily. The same species is also eaten at Kasoge (Nishida, 1974), but there was no mention of this pattern of seasonality. Afzelia bipindensis is eaten in Cameroon by chimpanzees (Gartlan and Struhsaker, 1972) and this too has a tough pod but no mention of its seasonal consumption was made. Similarly, Suzuki (1969) mentioned another species of Afzelia as being eaten in the Kasakati Basin, but did not describe seasonal consumption.

All other foods with their seasons and relative percentage frequencies in faeces are shown in Table 4.

A point must be made about seasonality and the importance of foods in the diet. The results discussed above come from the frequency with which these foods are found in faeces. Presence or absence alone is not sufficient to determine importance: the food must be eaten in appreciable quantities as well. Since we note quantities, at least relative to the faecal sample, this should be testable. Two problems arise however. The first is that the ratio of weight of fruit remains in faeces to their fresh weight was not measured, as mentioned earlier, so that comparisons cannot be made between fruits. The second problem is that no matter how accurate the ratio of raw weight to the weight of remains in faeces that one might obtain, the possibility of

Figure 12. Seasonal variation in consumption of *Afzelia africana* seeds.

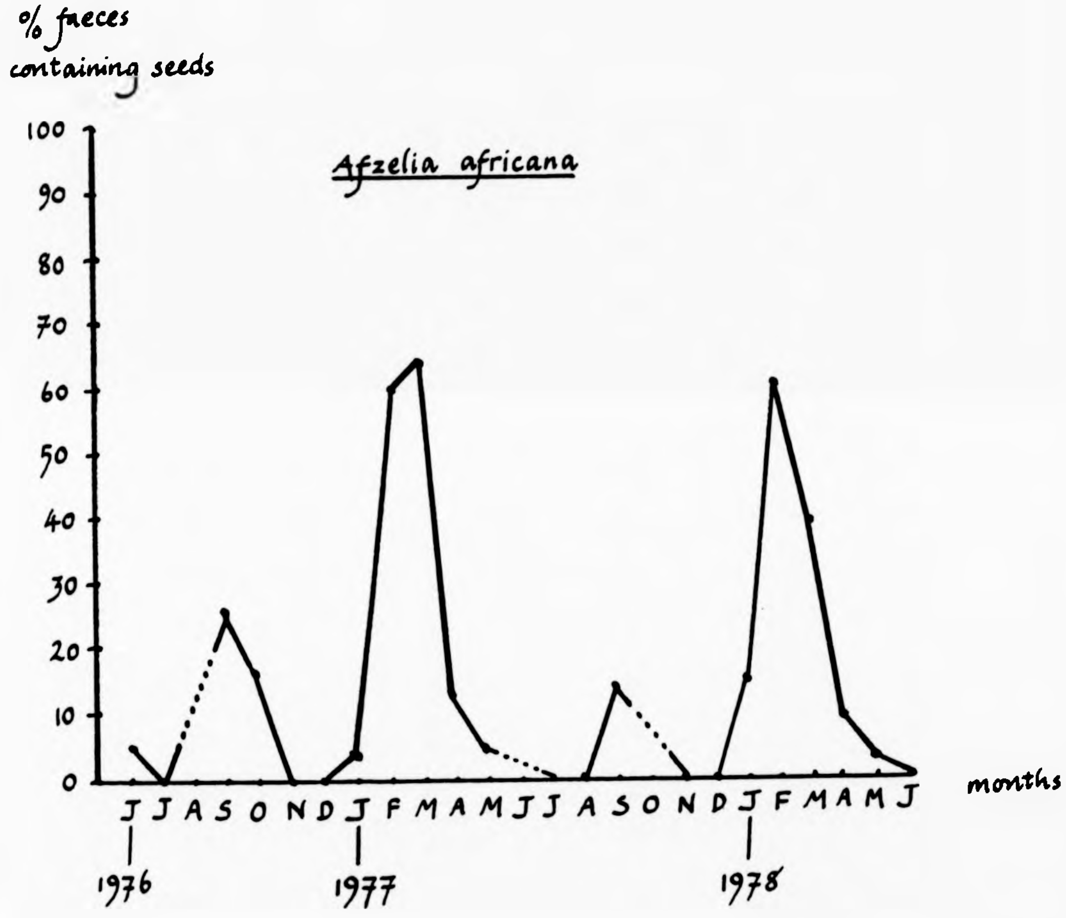


Table 4. Vegetable foods and their percentage frequences in faeces.

FOOD		1976						1977										1978							
	Part	June	July	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	July	Aug	Sept	Nov	Dec	Jan	Feb	March	April	May	June	Overall %	Rank
Adansonia digitata	F & S			47	72	90	95	89	10	6	22	21		20		83	84	85	72	55	22	11		40	3
Afzelia africana	S	6		27	17			4	60	65	13	4			14			15	61	40	9	2		15	7
Annona senegalensis	F													20										1	34
Ceiba pentandra	S										26	4							6	10	47	11		5	21
Cissus populnea	F			20	23											17								3	25
Cola cordifolia	F		16									92	83								72	44		14	9
Combretum tomentosum	F										4													0.2	40
Cordia myxa	F											21					13	15	6			4		3	25
Diospyros mespiliformis	F						50	93	75	12		8	6				68	85	6	25	3			20	5
Ficus spp.	F	10	10	53	100	100	95	89	50	100	91	42	67	20	29	83	87	92	28	75	84	53		62	1
Garcinia ovalifolia	F		2																					0.1	41
Grewia lasiodiscus	F				50	20										100	16							8	13
Hannoa undulata	F								40															2	29
Hexolobus monopetalus	F													80	100									8	13
	Fl.																				22			1	34
Icacina senegalensis	F	2																						0.5	42
Landolphia heudelotii	F	18	60									4	83											8	13
Lannea spp.	F	35	9								4	46									38	33		8	13
Nauclea latifolia	F													20										1	34
Oncoba spinosa	F							4	55	18	4													4	23

Table 4 contd.

FOOD		1976										1977							1978					Overall %	Rank
		June	July	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	July	Aug	Sept.	Nov	Dec	Jan	Feb	March	April	May	June		
Oxytenanthera abyssinica	St.	59	60	20				4		6				100	14									12	10
Parkia biglobosa	S										22	38										4		3	25
	Fl										13													0.6	38
Piliostigma thonningii	F								15	59	35								94	75				13	10
Pseudospondias microcarpa	F									41	96	4												6	18
Pterocarpus erinaceus	Fl								30	6														2	29
Saba senegalensis	F	98	100							47	9	71	83						50	70	62	84	100	40	3
Sapotaceae indet.	F	14	29									49	17				3					2		5	21
Spondias mombin	F			100	61							4		60	100									15	7
Strychnos spinosa	F	12	2				18										6							2	29
Tamarindus indica	S					60	50	11	6								84							10	12
Vitex madiensis	F				72																			3	25
Unknown (109)	F										4										31			2	29
Zizyphus sp. (1)	F						5	4	5	12														2	29
Zizyphus sp. (2)	F															15	13	23						4	23
Unidentified seeds		2	2	22		5	5	33	45	6	16				45	17		15						6	18
Unidentified flowers		2		7																				0.4	39
Unidentified bark																17								0.8	37

Table 4 contd.

FOOD	1976						1977										1978						Overall %	Rank
	June	July	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	July	Aug	Sept	Nov	Dec	Jan	Feb	March	April	May	June		
Unidentified stems/ shoots									6									50	5		11	78	7	17
Unidentified grass			60	22	5	23		10				11				3							6	18
Unidentified fibre	14	10	7		10	18		15	18	30	42	83		57	67	6	8			3			18	6
Unidentified leaves	53	76	6I	22	15	55	43	70	41	87	25	89	40	14	67	55	31	50	94	75	73	78	55	2
TOTAL vegetable items	13	12	11	9	8	10	10	13	16	15	17	9	8	8	9	12	9	10	9	12	12	3	-	-

F = fruit
Fl. = flower
S = seed
St. = stem

remains of individual differences in chimpanzees to do with the number of seeds that they spit out or swallow. This might vary seasonally with the size of the fruits and their stones. Young chimpanzees may spit out seeds that adults swallow, and adults may show differences depending on how hungry they are and how quickly they eat. All that is stated here, then, is that all the first-ranking foods (by frequency/month) are eaten in considerable quantities relative to other items in the samples.

8 (iii) Seasonal variation in the consumption of insects

Insects appearing in faeces are represented by the month in Figure 13. As may be seen in the histograms, there are peaks in the frequencies of termites and weaver ants during the months of May, June and July. These monthly differences were statistically significant (Kolmogorov-Smirnov one-sample tests: termites, $D = 0.43$, $p < 0.01$, $N = 131$; weaver ants, $D = 0.36$, $p < 0.01$, $N = 117$). Neither army, nor driver ants show any significant seasonality (Kolmogorov-Smirnov one-sample tests: army ants, $D = 0.17$, $p > 0.2$, $N = 19$; driver ants, $D = 0.14$, $0.05 < p < 0.1$, $N = 9$).

There are two types of insect consumption: either insects are eaten occasionally throughout the year or insects are eaten frequently over a short period. Seasonality in the eating of termites (*Macrotermes bellicosus*) also occurs at Gombe (Goodall, 1968), and there too, it coincides with the start of the rainy season. A plausible hypothesis for the chimpanzees' seasonal consumption of termites at Gombe and Mt. Assirik is that at the beginning of the rainy season, the termites are close to the mound's surface, and it is then advantageous to fish at the mound with delicate probes (McGrew *et al*, 1979). The occurrence of occasional termites in faeces at other times of the year may be due to the opportunistic catching of termites on the mound's surface, when it is being repaired. This seasonality is not found among chimpanzees in Rio Muni: there, termites are eaten all year-round, and the chimpanzees use different tools to obtain them (Jones and Sabater Pi, 1969; McGrew *et al*., 1979). Seasonal versus non-seasonal consumption of termites seems to be a function of the local climate.

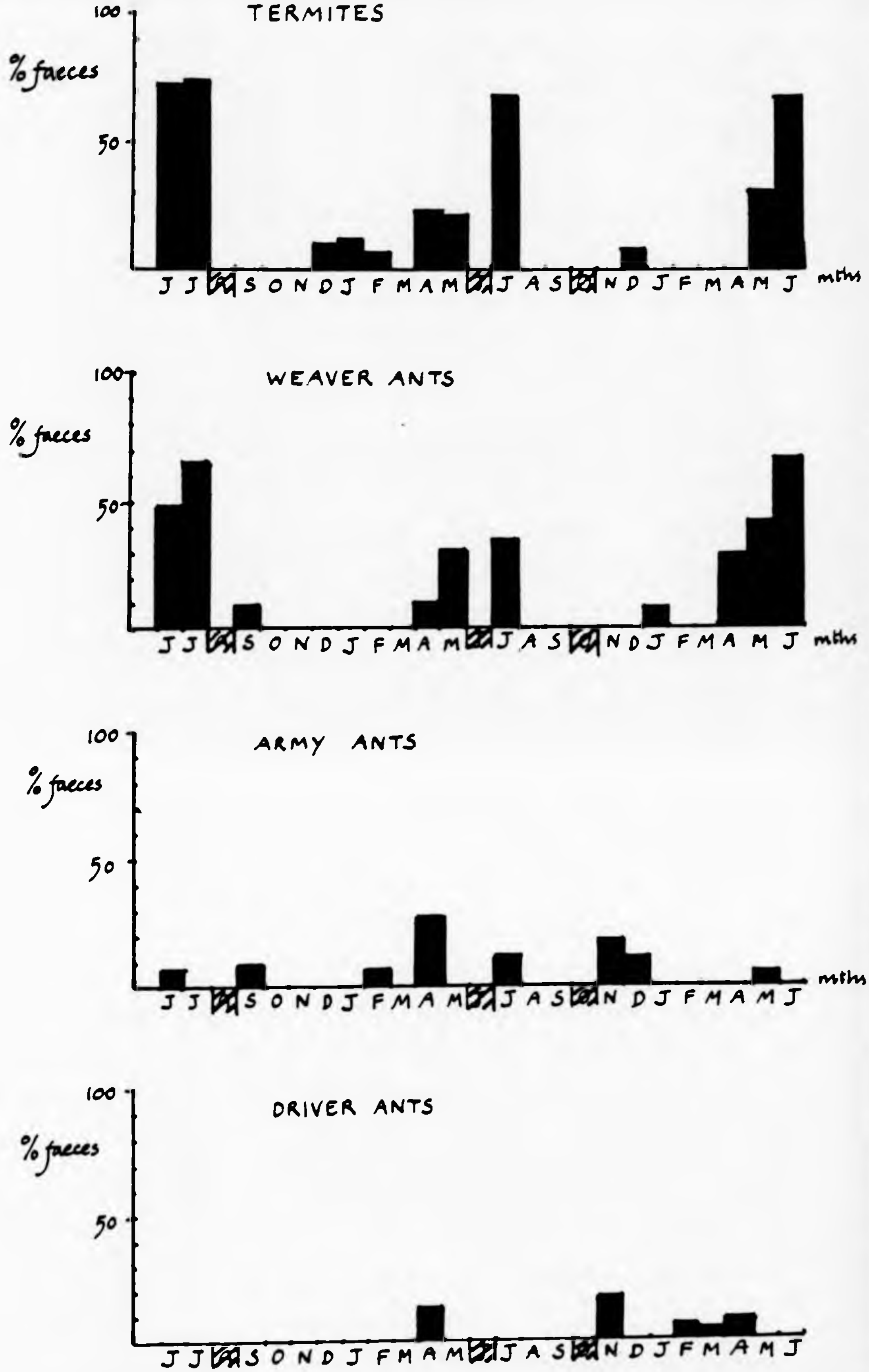


Figure 13. Occurrence of insects in faeces: slashed bars over certain months indicate insufficient data.

The case for weaver ants being eaten seasonally is unclear, since their nests are available year-round. Why should chimpanzees eat the contents of a nest at the beginning of the rainy season, but not at other times of the year? This is even more curious, however, when compared with the only other recorded seasonal consumption of weaver ants, at Gombe (Goodall, 1968). There chimpanzees eat weaver ants during the dry season.

Such a difference might be cultural: but since it is the timing of these ants' occurrence in the diet that varies, rather than their presence versus absence, or the manner in which they are caught, it is more likely to be related to the chimpanzees' nutritive needs, or to the natural history of the weaver ants. Although the workers, and occasionally the queens, of the weaver ant colony were found in faeces, it might be that chimpanzees consumed other developmental forms of the weaver ants, probably the soft-bodied and easily digestible larvae or pupae, which did not leave traces in the faeces. If this were so, then perhaps the contents of the nests were eaten when larvae were most abundant.

According to Ledoux (1950), workers in the weaver ant colonies can withstand high temperatures and low humidities, but eggs, larvae, and pupae must develop in conditions of high humidity. To a large extent the weaver ant colony can itself maintain these conditions by means of the transpiration of the living leaves from which the nest is constructed (see Fig. 14). Presumably, however, the humidity within the nest can only be maintained at the optimum of 95% (see Ledoux, 1950, p. 357) when the conditions outside are not too dessicating. Thus it may not be possible to maintain 95% humidity at Mt. Assirik during the dry season, when humidities fall as low as 9% (see Ch. 3). In the climate of Mt. Assirik, weaver ant reproduction probably peaks near the beginning of the rainy season when humidities rise.

At Gombe, however, chimpanzees eat the contents of these ant nests in the dry season, and during different calendar months. If this is also because many larvae are present, then they must be under the optimal conditions in

Figure 14. A weaver ant nest.

that climate. The humidities of the dry season do not fall as low as those at Mt. Assirik, only down to about 44% (Wrangham, 1975). The weaver ant nest can probably withstand this external dryness. This does not explain why eggs should be laid at this time of year rather than at any other. A clue comes from another of Ledoux's findings: the development from egg to imago occurs more quickly under higher temperatures. With air temperatures of 24 - 25°C this development takes 39 days: at 27 - 30°C the time taken is only 28 - 29 days. At Gombe, air temperatures are highest in August and September when they reach around 30°C (Wrangham, 1975). Thus optimal conditions for egg and larval growth should be at this time of year. At Mt. Assirik, the daily maxima reach at least the low 30's°C throughout the year (see Ch. 3), and the critical factor is most likely to be the onset of higher humidity.

Thus it is proposed that chimpanzees eat the contents of weaver ant nests when larvae are present. These develop under optimal conditions of heat and humidity. Such conditions exist around August and September at Gombe, and about May and June at Mt. Assirik. This proposition should be tested by examining the contents of weaver ant nests throughout the year at both sites, and by close observation of the weaver ant forms that the chimpanzees eat.

Weaver ant nests are gathered and eaten by reintroduced chimpanzees in Gabon. There Hladik (1973) found nests containing higher proportions of immature than mature ants. Presumably the constant heat and humidity of the site (Hladik, 1973) allow ants to reproduce all year round. Chimpanzees there do not eat weaver ants seasonally (Hladik, 1977).

From faecal evidence, army ants and driver ants are eaten only sporadically. It is assumed that chimpanzees eat these insects opportunistically when they happen to come across them. While out in the field ourselves, we rarely came upon them: at an estimate, we saw army ants about 5 times a year and driver ants about 10 times a year.

8 (iv) Seasonal consumption of honey, bees and meat

There appears to be no seasonality in the consumption of either honey and bees. (see Fig. 15). There is also no apparent seasonal consumption of meat, with 6 cases occurring in the wet season months (N = 10? and 6 cases in the dry season months (N = 17). Meat is eaten rarely and sporadically, and this concurs with the conclusion that the catching of prey is fortuitous (see Fig. 16).

9. Inter-annual variation in the diet

There has been little inter-annual variation in the diet at Mt. Assirik, with only two notable foods differing over the two years. One is the fruit of *Pseudospondias microcarpa* that occurred in 40% of faeces in March, and 96% of faeces in April, 1977, but was not found at all in 1978 (see Fig. 10). Flowers appeared on the trees in 1978 but shrivelled up and dropped off before the fruit formed. A local botanist thought the preceding season's low rainfall was responsible for the failure. In 1978, in place of this fruit, chimpanzees started to eat *Cola cordifolia* and *Saba senegalensis* fruits earlier than they had done the previous year. In April, 1978, 62% of faeces contained *Cola* fruits, whereas none had contained them in April, 1977. *Saba* fruits were found in 50% of faeces in February, 1978, compared with none in 1977.

Hexolobus monopetalus fruits were found in 80% and 100% of faeces in August and September 1977, but were never found in faeces in 1976. Although the total number of faecal samples is small for these months the complete absence in 1976 is remarkable. No phenological data are available for the relative abundance in the two years, but it seems likely that the variation between years was because the fruit was more plentiful in the second year.

10. Diet, feeding behaviour and the use of habitats

Although we have no record of time spent by chimpanzees feeding in each type of vegetation, a careful estimate can be arrived at by looking at

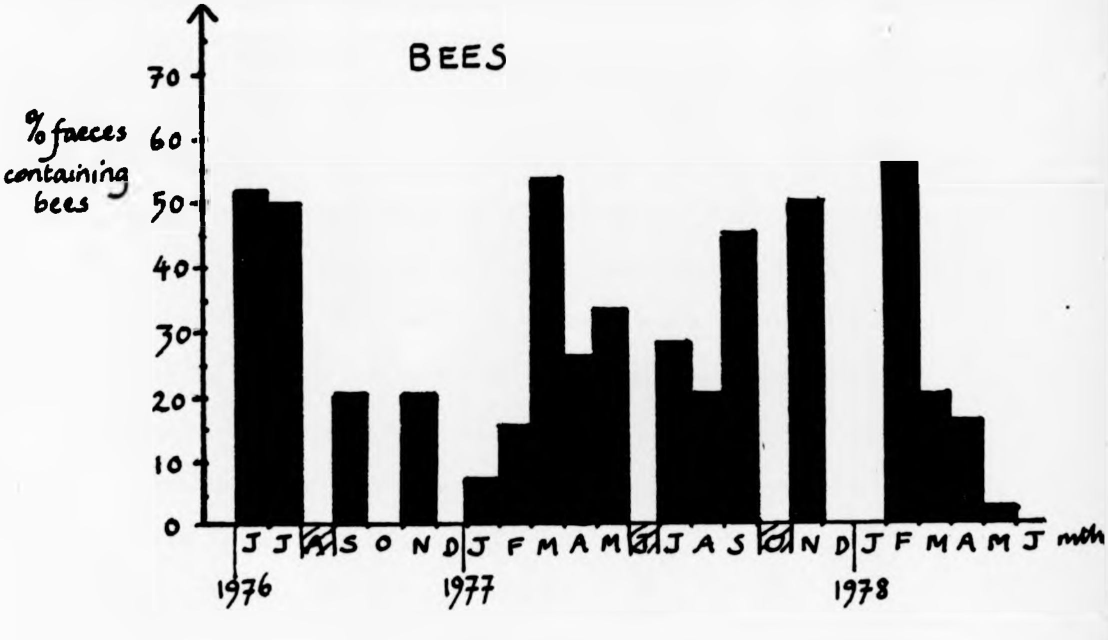


Figure 15. Occurrence of bees in faeces: slashed bars over some months indicate insufficient data.

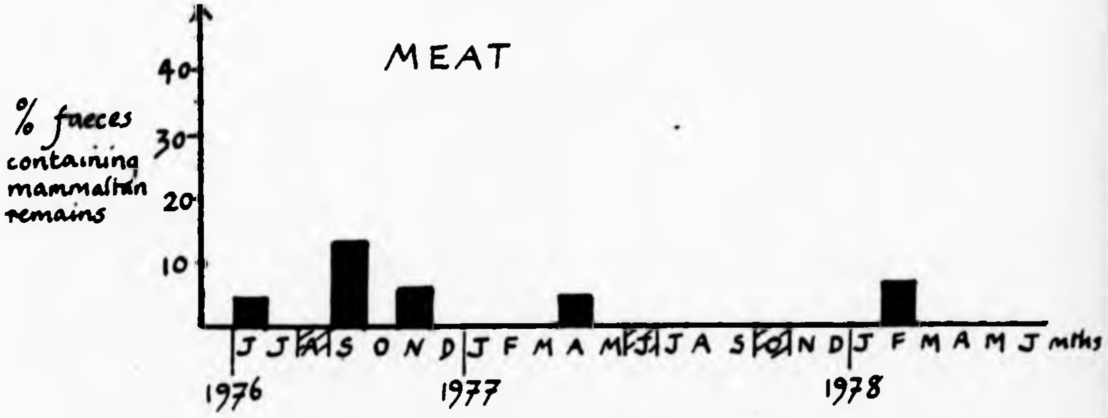


Figure 16. Occurrence of mammalian remains in faeces: slashed bars over some months indicate insufficient data.

principal items in the diet and their sources. Foods which are eaten occasionally may also determine where chimpanzees forage, if they contain essential minerals (Hladik, 1977) but it is assumed for this estimate that they are less important than the frequently eaten foods. Table 5 shows foods ranked 1 - 5 in terms of of frequency per month, with their main type of habitat beside them. Species occurring in more than one type of vegetation, score equally in both. This is admittedly a crude reckoning, but the results show that most species are available in woodland (47%), then forest (35%), then grassland (16%) and finally bamboo (2%). This same ordering holds for both wet and dry seasons.

Direct observation of feeding chimpanzees shows a different pattern throughout the year. Percentages of observations are as follows: forest 47%, woodland 38%, grassland 13%, bamboo 2% (N = 121). The proportions of grassland and bamboo are similar for the food source and observation analyses, but the forest and woodland are reversed. A closer examination of these direct observations, however, reveals a big seasonal difference: of 35 wet season observations, only 6% were in forest, 54% were in woodland, 37% were in grassland, and 3% in bamboo. Thus the overall predominance of forest observations is a result of dry season data (N = 86) smothering the wet season data (N = 35), see Table 6.

It seems that although the availability of food remains proportionally the same in each type of vegetation over the seasons, chimpanzees exploit the woodland and grassland areas more in the wet season because temperatures are generally lower (Ch. 3). Another pertinent factor is that these primarily deciduous areas are leafed and have both shade and water at this time (Ch. 5). Thus in the dry season, chimpanzees are restricted to the limited areas close to shade and water during the day, but in the wet season, they seem to be unrestricted. The results of these feeding observations concur with the general results of ranging, described in Chapter 6. They further suggest that the ranging patterns are not determined by the seasonal availability of food, but are more likely to be related to the

Table 5. The most common items in the diet and the types of vegetation in which they most often occur.

	MONTH	No.of samples	Ranks by frequency of occurrence in faeces					Habitat			
			First	Second	Third	Fourth	Fifth	F	W	G	B
1976	June	51	*Saba sp.* F W	Termites W	*Oxytenanthera sp.* B	Leaves F W	Honey F	3	3		1
	July	45	*Saba sp.* F W	Leaves F W	Weaver ants W	*Oxytenanthera sp.* B	*Landolphia sp.* F	3	3		1
	Sept.	15	*Spondias sp.* W G	Leaves F W	*Adansonia sp.* W G	Grass ?	*Ficus sp.* F W G	2	4	3	
	Oct.	18	*Ficus sp.* F W G	*Adansonia sp.* W G	*Vitex sp.* W	*Spondias sp.* W G	*Grewia sp.* W	1	5	3	
	Nov.	20	*Ficus sp.* F W G	*Adansonia sp.* W G	*Tamarindus sp.* W	Honey F	*Grewia sp.* W	2	4	2	
	Dec.	22	*Ficus sp.* F W G *Adansonia sp.* W G		Leaves F W	*Tamarindus sp.* W *Diospyros sp.*		3	4	2	
1977	Jan.	28	*Diospyros sp.* F	*Adansonia sp.* W G	*Ficus sp.* F W G	Leaves F W	Unident.seeds ?	3	3	2	
	Feb.	20	*Diospyros sp.* F	Leaves F W	*Afzelia sp.* W	*Oncoba sp.* W	*Ficus sp.* F W G	3	4		
	March	17	*Ficus sp.* F W G	*Afzelia sp.* W	*Piliostigma sp.* W	Honey F	*Saba sp.* F W	3	4	1	
	April	23	*Pseudospondias sp.* F	*Ficus sp.* F W G	Leaves F W	*Piliostigma sp.* F W	Honey F *Ceiba sp.* F	5	3	1	
	May	24	*Cola sp.* F	*Saba sp.* F W	Sapotaceae indet. F	*Lannea sp.* W	*Ficus sp.* F W G	4	3	1	
	July	18	*Saba sp.* F W *Cola sp.* F		*Landolphia sp.* F	Leaves F W	Termites W	4	3		

Table 5 contd.

MONTH	No. of samples	First	Second	Third	Fourth	Fifth	Habitat F	Habitat W	Habitat G	Habitat B
Aug.	5	*Oxytenanthera sp.* B	*Hexolobus sp.* W	*Spondias sp.* W G	Leaves F W	*Adansonia sp.* W G *Annona sp.* W *Ficus sp.* F W G *Nauclea sp.* W	2	7	3	1
Sept.	7	*Spondias sp.* W G *Hexolobus sp.* W		Honey F	Unident.seeds ?	*Ficus sp.* F W G	2	3	2	
Nov.	6	*Grewia sp.* W	*Adansonia sp.* W G	*Ficus sp.* F W G	Leaves F W	*Zizyphus sp.* W	2	5	2	
Dec.	31	*Ficus sp.* F W G	*Adansonia sp.* W G	*Tamarindus sp.* W	*Diospyros sp.* F	Leaves F W	3	4	2	
1978 Jan	13	*Ficus sp.* F W G	*Adansonia sp.* W G	*Diospyros sp.* F	Leaves F W	*Zizyphus sp.* W	3	4	2	
Feb	18	*Piliostigma sp.* W	*Adansonia sp.* W G	Leaves F W	*Saba sp.* F W	Honey F	3	4	1	
March	20	Leaves F W	*Ficus sp.* F W G	*Piliostigma sp.* W	*Saba sp.* F W	*Adansonia sp.* W G	3	5	2	
April	32	*Ficus sp.* F W G	Leaves F W	*Cola sp.* F	*Saba sp.* F W	*Ceiba sp.* F	5	3	1	
May	45	*Saba sp.* F W	Leaves F W	*Ficus sp.* F W G	*Cola sp.* F	*Strychnos sp.* W	3	3		
June	27	*Saba sp.* F W	Leaves F W	Termites W Weaver ants W			2	4		
						TOTALS	64	85	30	3

Table 6. The distributions of important foods and sightings of feeding chimpanzees by habitat and season.

Distributions	Season	N	Type of vegetation				
			F	W	G	B	P
Locations of important foods	Wet	65	29%	49%	17%	5%	-
	Dry	117	39%	45%	16%	-	-
	Overall	182	35%	47%	16%	2%	-
Sightings of feeding chimpanzees	Wet	35	6%	54%	37%	3%	-
	Dry	86	64%	31%	4%	1%	-
	Overall	121	47%	38%	13%	2%	-

distribution of water, and extreme air temperatures.

Chapter 9.

NESTING

1. Introduction

It is a remarkable feature of the behaviour of the great apes that in the wild they fabricate comfortable nests, or cushions of vegetation, upon which to sleep at night. They are the only higher primates which do so. Hediger (1977) called these "sleeping nests" to distinguish them from nests made by other animals for other pruposes, e.g., breeding, or as a permanent home. Nests made by gorillas are often on the ground (Schaller, 1965) but those of orang utans (MacKinnon 1974) and of chimpanzees (Nissen, 1931; Goodall, 1968; Jones and Sabater Pi, 1971) are made off the ground in vegetation. Similar nests are made occasionally during the day when apes are resting. This chapter will be concerned mainly with nests made by chimpanzees for sleeping at night, since day nests were only rarely found.

No one has carried out a comprehensive, systematic study of nests, either across habitats or within one. During this study, nests were recorded in detail, and it is hoped that future field studies will make use of these records for comparative studies.

Captive chimpanzees do not all spontaneously build nests when given the appropriate materials. Though the effects of experience and maturation have not been systematically inevestigated, some complex interaction is suspected (Bernstein, 1962). This being the case, variation is expected to occur across populations, either according to differences in habitats, or as a function of culturally divergent methods of construction. Differences of habitat, such as in types or heights or spacing of trees, might give rise to differences in the nests built in them.

This chapter will first describe what we have seen of chimpanzees building nests, and of their night-time activities; it will compare this behaviour with that of other chimpanzees. The chapter will then go on to look at the

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2. Building nests

We observed chimpanzees building nests on 6 occasions over the course of the study. A total of 11 nests were seen during part or all of their construction.

The times of beginning of construction ranged from 1649 to 1922 hours GMT. The sun sets at about 1900 hours in the wet season and 1930 hours in the dry season. The median time of beginning construction was 17.38 hours (N = 9). The data cannot be tested for seasonal differences because the samples are small (N = 2,dry season; N = 7, wet season), and because they are not independent events, since they come from members of the same party in most cases, and one individual may be prompted into building a nest by the sight of another in his party doing the same. It has been found elsewhere that the time of beginning nest construction varies seasonally with nests in the wet season being made earlier than those of the dry season (Goodall, 1968; Izawa and Itani, 1966). This seemed to be related to rainfall and cloudiness rather than the time of sunset (Goodall, 1968).

Activities preceding the building of nests also varied. Sometimes chimpanzees nested in the same place where they had been feeding. Sometimes they had been travelling a considerable distance immediately before nesting.

The actual building of the nest took, on average, only 4 minutes (range = 2 - 7 minutes, N = 7). The times reported elsewhere are shown in Table 1. It can be seen that the other reported ranges of times are similar.

We saw chimpanzees constructing nests much as other reports have described (Nissen, 1931; Reynolds and Reynolds, 1965; Izawa and Itani, 1966; Goodall, 1968). Differences in the finished nests will be discussed in the second section, but the behaviour described below for nesting by wild chimpanzees at Mt. Assirik is consistent with the above reports.

TABLE 1. A comparison of features of nests and nesting behaviour in 6 different populations.

Study	N	Largest N in 1 tree		Average height (m)	Range of heights	Shape	Fruit ever in nest	Faeces ever in nest	Re-use	Day nests	Time (mins.) spent building	Body position
		any age	same age									
Reynolds & Reynolds 1965	259	?	?	?	3 - 30	?	?	?	?	yes	1 - 5	?
Izawa & Itani 1966	491	?	5	19	5 - 40	oval	?	no	yes	yes	?	lying on back
Goodall 1968	384	?	10	14.4	5 - 24	?	?	no	yes	yes	1 - 5	lying on back or side
Jones & Sabater Pi 1972	?	?	?	"about 3 - 10"	3 - ?	?	?	?	?	?	?	?
Nissen 1931	?	13	10	11.7	4 - 32	oval	yes	no	yes	yes	3	lying on back or side
This study	163	21	7	11.3	2 - 40	oval	yes	no	yes	yes	2 - 7 (N = 7)	lying on back or side

The method of building nests is to bend over branches, standing on each one as the next is bent over it. The foundation of this structure is often the crotch of a tree. At Mt. Assirik, on average, 3 of these main branches (thicker than 2.5 cm diameter) are used. After this base has been made, smaller branches are bent inwards, and, finally, the nest is lined with leafy twigs. The lining process may continue sporadically for some time. Once an adult male built and lined a nest, then reclined on his back and rested: 47 minutes later he added more leafy twigs to the nest.

When settling down for the night, chimpanzees at Mt. Assirik lay on their backs or sides in the nest. Where details are given, this is the case elsewhere (see Table 1). Chimpanzees are known to sleep singly in nests with the exception of mothers and unweaned offspring. At Mt. Assirik, on 3 occasions, adult females were seen to build nests, and their small infants lay down beside them. Another adult female was seen to build a nest, and a juvenile accompanying her built a nest less than 5 m away. Goodall (1968) reported that juveniles usually nest in separate nests but remain close by their mothers.

In general, chimpanzees build fresh nests each evening, but the occasional old nest which had been freshly lined with green branches and leaves was found. Once an old male was seen to make a nest and then later make another nearby; there was no apparent reason why the first nest was unsuitable. Re-use of old nests was seen by Nissen (1931) and Izawa and Itani (1966), and both re-use and the abandonment of a nest followed by the building of a second was seen by Goodall (1968).

3. Night-time Activity

During the night, chimpanzees sometimes called, giving pant-hoot choruses, screams, and waas. Occasionally there were exchanges of these calls when two groups nested more than 100 metres apart. These vocalisations were also elicited by the calls of lion and leopard. Then chimpanzees also gave wraaghs. When a leopard was a temporary resident in Lion Valley, and called regularly during the night, the chimpanzees diminished their vocal response to the sawing of the leopard unless it was very close to them, but continued to respond to the coughs of the leopard. They did not respond to a wide range of other animal calls at night, e.g., elephant, jackal and hyaena.

Chimpanzees rarely travelled at night, although they moved off promptly at first light. However, in 1978, two extraordinary incidents of activity at night occurred. Once in April and once in November,,at about midnight, wild chimpanzees attacked the chimpanzees of the rehabilitation project, by approaching the camp and fighting with those rehabilitates which had descended from the trees to greet them. In the morning no nests were found in Stella's Valley, suggesting that the wild chimpanzees either had not made nests that night but had slept in the area, or else had travelled some distance in the dark to approach the rehabilitation camp. Izawa and Itani (1966) reported that chimpanzees in the Kasakati area travelled at night, although this was not actually seen. The assertion was made on the basis of vocalisations. Goodall (1968) also reported activity at night when chimpanzees came to feed on the bananas at the artificial feeding point at Gombe. This was not a natural situation, though, since the food was highly prized and an individual may have been subjected to fierce competition during the day, so that night-time collection of bananas was a more comfortable alternative. In general, it is unusual for chimpanzees to travel at night.

4. Arising and leaving nests

In most cases, it was too dark to see what occurred when chimpanzees woke up and left their nests. On one occasion, however, a chimpanzee was observed as he slept, and his behaviour upon wakening seen, Three minutes before he awoke, there were screams and the sounds of branch movement, urination and defecation from other chimpanzees nearby. Then the adolescent male under observation stretched himself and rolled over from the supine position, so that he was crouching with his buttocks over the edge of the nest. He then urinated and defecated and immediately descended from the nest to the ground. This procedure took little more than a minute, and resembles that described by Goodall (1968).

In the four cases when we could not see the leaving of the nests but were able to see chimpanzees immediately after the sounds of nest-leaving, their first activity was feeding. In three of the cases they fed for less than an hour before travelling: in the fourth, they fed all morning in the vicinity of the nest-site. In all cases, calling accompanied their rising.

Chimpanzees habitually urinated and defecated upon wakening. Even when this could not be seen, it could usually be heard, and the solid evidence in the form of faeces and urine below the nests confirmed this. There was no evidence of the nests having been soiled and this concurs with other findings (see Table 1). In this respect, chimpanzees differ from gorillas. The extent of the habit of defecation inside the nest varies even within subspecies of gorilla. Goodall (1979) proposed this to be related to night temperatures, with flattened dung being used as insulation in the nest. MacKinnon (1974) reported no evidence of orang utans defecating in their nests.

It seems curious that chimpanzees should apparently take care not to foul their nests, when nests are generally used only once. If they were used repeatedly, it might be more advantageous to defecate outside the nest to avoid possible reinfection by parasites. It may be a generalised habit of avoiding contact with faeces, since during the day chimpanzees often defecate from a small height, e.g., off a fallen log or a tree root. It may be that new nests every night are a comparatively recent introduction, and that at one time chimpanzees ranged less widely and reused nests more frequently.

As mentioned in the introduction, chimpanzees sometimes make nests during the day. These are used for resting and day-time sleeping. At Mt. Assirik they were shallower and smaller than night-nests. Some were made on the ground by bending over branches and covering them with leafy twigs. One day-nest consisted of no more than 3 or 4 leafy twigs laid in a heap on a stout branch. This was probably the result of a young individual playing at nest-making, since it scarcely functioned as a cushion. It is possible that a proportion of the day-nests were the result of play. Day nests were made both on the ground and in trees, as has been found in several other populations (see Table 1).

5. The construction of nests

5.(i) Habitat

As was shown in Chapter 6 on ranging, most nests are found in woodland. The next most commonly used type of vegetation is forest, then grassland. Nests are only rarely made in bamboo or on plateaux.

Woodland may be used most often simply because it covers more surface area than any other type of vegetation at Mt. Assirik, so that by chance, if woodland is at all suitable, it should have the most nests. The sheer extensiveness of woodland may be important, but for a different reason: it allows chimpanzees to nest in a new location every night. If they restricted their nesting to forest, then they would have to nest in the same small areas repeatedly. This might attract predators or lead to a local increase in parasites. (The importance of baboons' changing sleeping sites as a means of avoiding parasites was pointed out by Hausfater and Meade, 1978). All chimpanzees studied so far, nest in scattered locations, although some sites may be used more than once.

Woodland may also be attractive because of the array of species available. This would permit individual preferences to be fulfilled when a party of chimpanzees nests together. To examine this question, samples were taken of nests, of which the species of tree was identified. Samples of the first

150 nests in forest, woodland and grassland, recorded after October 1st 1976 were analysed. The diversity of species included was greatest in woodland where the species numbered 17. The sample from forest comprised 12 species and that from grassland only 4 species. In all samples, however, one species predominated (see Figs.1&2) having about, or more than, 50% of nests. These were Pseudospondias microcarpa in the forest, and Pterocarpus erinaceus in the woodland: in grassland, Pterocarpus erinaceus had 79% of nests.

From Chapter 5, the diversity of species, as sampled by transects, was greatest in the forest. Thus the greater use of woodland for nesting could be because particular properties of the woodland species make them preferable. Woodland species are mainly deciduous and have thinner, softer leaves than the mainly evergreen trees of the forest, many of which have sclerophyllous leaves. The predominant use of woodland for nesting probably results from a combination of these factors and the influence of feeding and general ranging strategies.

5.(ii) Species of tree used

Figs.1&2 show that in each type of vegetation, chimpanzees favour a small number of tree species. Rank-orders of these species are not correlated with their order of frequency on the transect samples. In woodland, the first six nest species could be tested against their transect frequencies: no significant correlation was found (Kendall Rank Correlation coefficient; $r = 0.13$, $S = 2$, $N = 6$, $p > 0.408$): in forest, the first nine nest species were tested ($r = -0.28$, $S = 1$, $N = 9$, $0.46 < p < 0.54$). Some lower-ranking nest species did not occur on the transects of forest and woodland, and none of the grassland nest species occurred on the sample of 500 metres of grassland. These results show preferences for species of trees as nesting material, and these are not related to their frequency in the type of vegetation. This is the first time that this has been demonstrated in any ape population.

It is interesting to note that the most popular species in woodland is also

Figure 1. The tree species used for nesting in woodland (N = 150 nests)

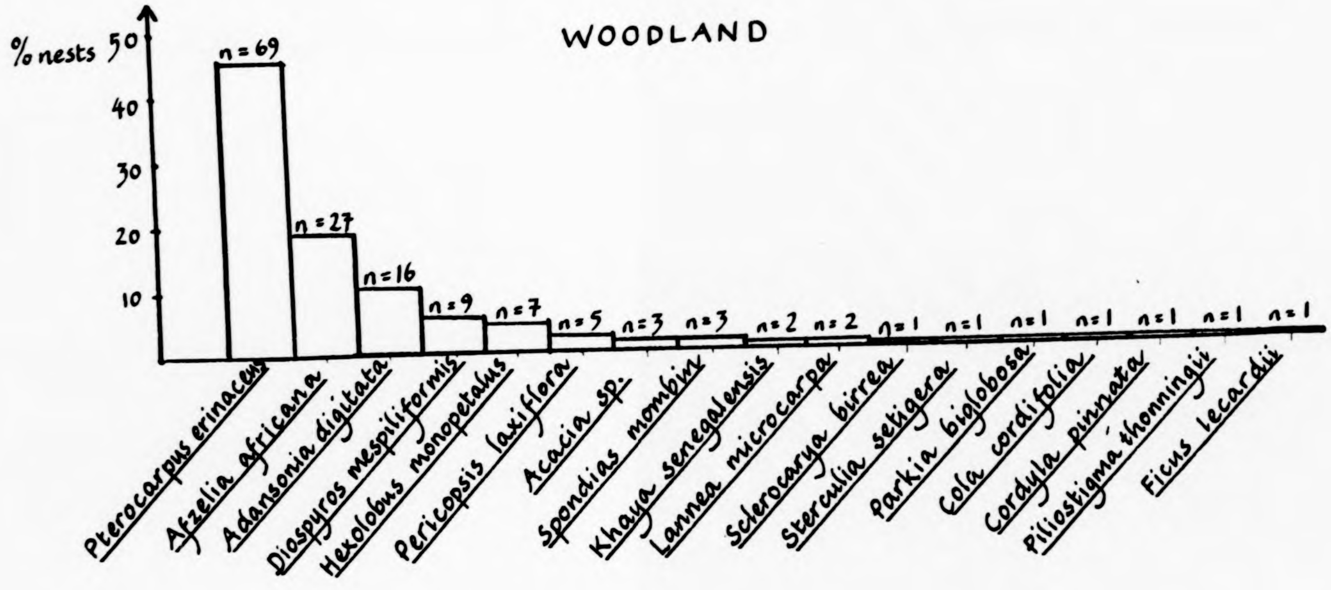
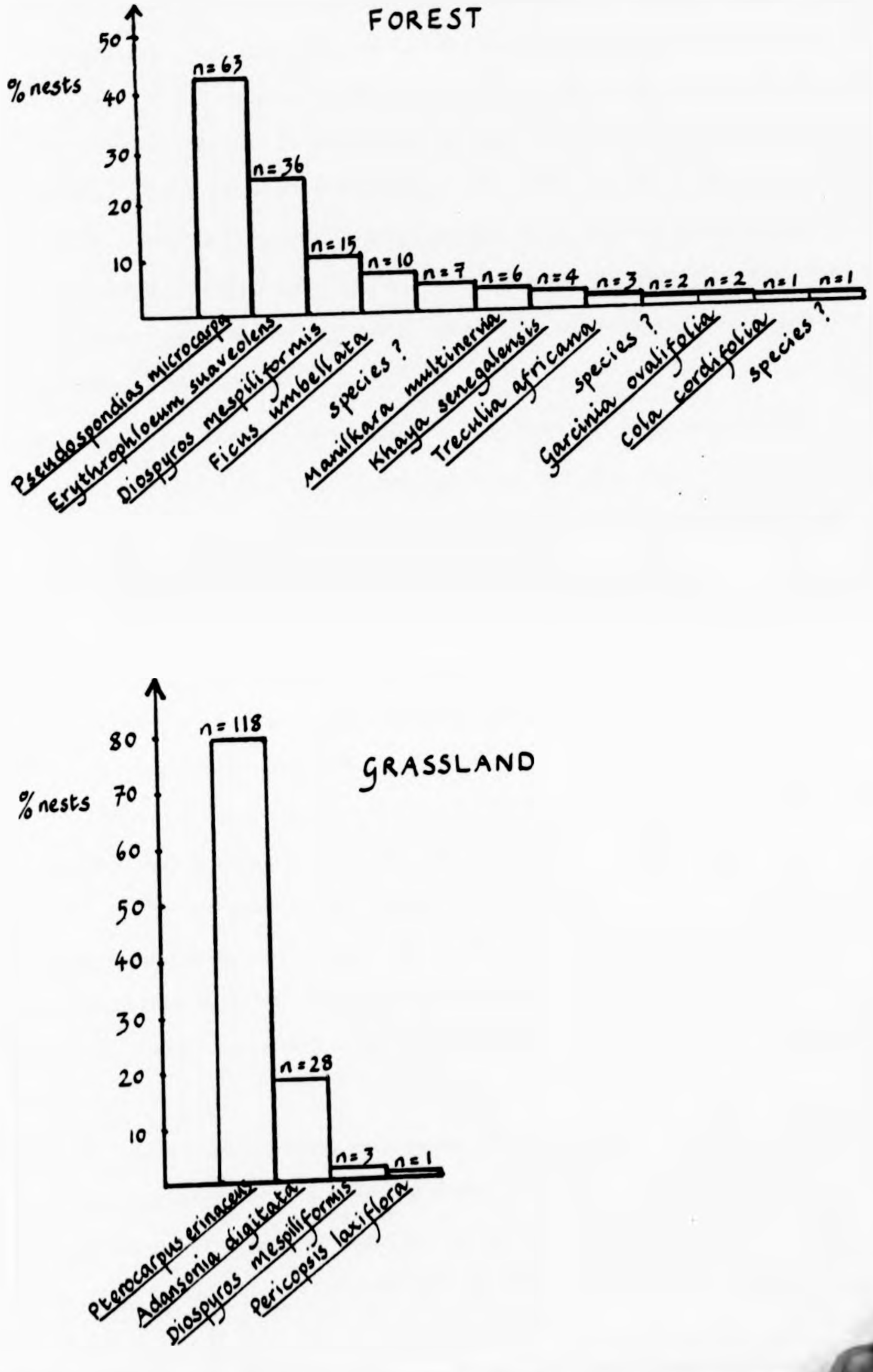


Figure 2. The tree species used for nesting in forest (above) and grassland (below): N = 150 nests in both samples.



the most popular species in grassland. The frequent use of this tree is not surprising in woodland, since Pterocarpus erinaceus was the second most frequent species on woodland transects, but in grassland it did not even occur on the transect. Its frequent use for nesting there suggests that chimpanzees seek it out because it is more suitable than other grassland species. This is probably because it grows much taller than other grassland species and because it has abundant soft leaves. The only species found in all three samples of nests is Diospyros mespiliformis, which usually grows beside seasonal water courses in all types of vegetation. It seems to be universally suitable for nesting, probably because it is evergreen and abundantly leafed throughout the year.

An ideal tree for nesting is presumably one which has many soft leaves attached to thin pliable twigs. Neither the trunk nor branches should be spiny. Branches should be pliable so that they can be bent in to form the base of the nest, and the tree should be between 10 and 20 metres tall (see next section).

5.(iii) The height of nests and the height of trees

The only records of chimpanzees sleeping on the ground overnight came from Kortlandt (1967) and Rahm (1967). In the first case, where 13% of nests were on the ground at Beni, Belgian Congo, chimpanzees lived close to human habitation and were protected. Perhaps this rendered the safety of trees unnecessary. In the second case, ground nests were made at another site in the Congo when chimpanzees spent the night in banana fields: other ground nests described by Rahm (small and without faeces nearby), may have been day nests. All other studies have found chimpanzees making night nests in trees.

Reynolds and Reynolds (1965) maintained that the height of nests was influenced by the height of trees in the area. A closer examination may reveal how the height of a nest is affected by the height of the tree which contains it. It may also be of interest to know how both measurements relate to the general height of woody vegetation in different habitats.

Data on nests were collected in two ways. The first was the general method of recording the age, location and species of tree for each nest encountered. The second method was more detailed: the characteristics of randomly selected nests were recorded on printed cards (see Ch. 4). Detailed notes on the height of the nest, its dimensions and spatial relation to other nests, as well as measurements of the tree, its species and relation to other trees were recorded. Also noted was whether there was an alternative route of escape from the nest other than by climbing down the trunk of the tree which contained the nest. The point of recording this feature was to assess the chimpanzees' regard for safety from predators when constructing a nest.

Table 2 summarises the results on the heights of both nests and trees. In all types of vegetation, the trees chosen for nesting are generally considerably taller than the mean height for woody vegetation. For example, the mean heights of woodland trees in which nests were found were 12.4m (dry season) and 12.6m (wet season), yet from transects (Ch. 5) only 17% of the trees were over 10m tall. It seems that chimpanzees prefer the tallest trees in each habitat for building nests.

For all types of vegetation and both seasons, the median of nest heights equalled the means shown in Table 2, when means were rounded to the nearest whole number. The exception was in the forest wet season sample, where the median, at 11m, was well below the mean. Table 2 shows that there was a wide range and much variance in the nest heights, partly accounted for by 2 nests made at the extraordinary height of 40m.

The range of heights of nests at Mt. Assirik is greater than those recorded elsewhere, despite the fact that the sample size was the smallest (see Table 1). This is possibly due to the diversity of types of vegetation at Mt. Assirik that allows nests to be built at many different heights. The overall mean of nest heights at Mt. Assirik is 11.3m (N = 163, range = 2 - 40); this is less than all other means in the published literature, except the

Table 2 . A comparison of statistics on the heights of trees and nests by habitat and season.

HABITAT		DRY SEASON				WET SEASON			
		N	$\bar{x}$	$s_{\bar{x}}$	range	N	$\bar{x}$	$s_{\bar{x}}$	range
	Tree heights	221	10.2	0.53	2 - 40	221	10.2	0.53	2 - 40
FOREST	Nest tree heights	51	15.1	1.04	7 - 23	22	19.9	1.57	7 - 40
	Nest heights	51	11.8	0.74	3 - 22	22	15.3	2.02	5 - 40
		mean proportional height = 0.78				mean proportional height = 0.77			
		N	$\bar{x}$	$s_{\bar{x}}$	range	N	$\bar{x}$	$s_{\bar{x}}$	range
	Tree heights	132	6.9	0.38	2 - 24	132	6.9	0.38	2 - 24
WOODLAND	Nest tree heights	47	12.4	0.48	2 - 25	33	12.6	0.51	7 - 21
	Nest heights	47	9.5	0.52	2 - 22	33	10.9	0.56	6 - 19
		mean proportional height = 0.77				mean proportional height = 0.86			
		N	$\bar{x}$	$s_{\bar{x}}$	range				
	Tree heights	48	3.5	0.25	2 - 10				
GRASSLAND	Nest tree heights	10	11.1	0.6	9 - 16				
	Nest heights	10	9.2	0.44	8 - 11				
		mean proportional height = 0.82							

general statement of Jones and Sabater Pi (1972), shown in Table 1, which is too vague for direct comparison.

Nests are built at a fairly consistent proportional height of the trees that contain them (see Table 2). The mean proportional height of all nests is 0.8 (N = 163). The only significant difference between habitat types and seasons in this feature was between the woodland dry and wet season samples (Median test: $\chi^2 = 3.97$, df = 1, $0.02<p<0.05$, N = 80). Chimpanzees may build their nests higher up the trees in woodland during the wet season because of the weather. When rain falls at night and chimpanzees become wet, the drying and warming effect of the morning sunshine may be important; thus chimpanzees may position themselves higher in the trees to take advantage of it. This strategy would be less effective in the forest, since there the foliage is more dense, with less opportunity to catch the rays of the sun in the nest. Unfortunately, a seasonal comparison in grassland is not possible because data are lacking for grassland in the wet season.

The heights of the nests were found to be dependent upon the type of vegetation in which they occurred. This was indicated by the significantly descending order of mean heights in forest, woodland and grassland. ($\chi^2 = 10.7$, df = 2, $p<0.01$, N = 163). This suggests that the heights of nests are dependent upon the heights of trees in the surrounding vegetation: and as was shown earlier, chimpanzees prefer the tallest trees within each type.

This pattern seems to extend across other populations of chimpanzees. Izawa and Itani (1966) recorded over 19% of nests in riverine forest where the mean height of trees was 20m (dry riverine forest) and 22m (wet riverine forest). The mean height of the nests they recorded was 19m (N = 384), suggesting that if chimpanzees there build nests at the same proportional height (the authors stated merely 'near the top'), they are building nests in the tallest trees of the forest. The results from Mt. Assirik and from Izawa and Itani (1966) suggest that chimpanzees prefer the tallest trees for nesting. They also support the common-sense conclusion put forward by general statement of Jones and Sabater Pi (1972), shown in Table 1, which is too vague for direct comparison.

Nests are built at a fairly consistent proportional height of the trees that contain them (see Table 2). The mean proportional height of all nests is 0.8 (N = 163). The only significant difference between habitat types and seasons in this feature was between the woodland dry and wet season samples (Median test: $\chi^2 = 3.97$, df = 1, $0.02<p<0.05$, N = 80). Chimpanzees may build their nests higher up the trees in woodland during the wet season because of the weather. When rain falls at night and chimpanzees become wet, the drying and warming effect of the morning sunshine may be important; thus chimpanzees may position themselves higher in the trees to take advantage of it. This strategy would be less effective in the forest, since there the foliage is more dense, with less opportunity to catch the rays of the sun in the nest. Unfortunately, a seasonal comparison in grassland is not possible because data are lacking for grassland in the wet season.

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Reynolds and Reynolds (1965) that the height of the nest is largely determined by the heights of the available trees. Unfortunately the mean heights of available trees are not given by Nissen (1931) or Goodall (1968), but on the basis of their mean nest heights (see Table 1) the means of the heights of trees at these sites should be higher than at Mt. Assirik.

5.(iv) Safety

Goodall (1968) mentioned that nests were generally not found in trees which had branches occurring lower than 10ft. (3m) off the ground. This is presumably because low branches facilitate access to the nest for predators with some climbing ability, i.e. leopards. At Mt. Assirik, of the 163 nests examined, 54 (33%) were built in trees with branches occurring lower than 3m off the ground. Since leopards are present at Mt. Assirik, and have been heard calling from chimpanzees' nesting sites, it seems somewhat daring of them to nest in such accessible trees. However, examination of claw marks following an encounter with a leopard (Gandini and Baldwin, 1978) revealed that a young adult leopard had climbed the vertical trunk of a tree, whose lowest branch occurred at a height of 8 metres. Thus leopards probably have access to most trees. If chimpanzees wish to protect themselves from leopards at Mt. Assirik, they must seek other means.

Possible escape routes from the nests to the ground, other than by the trunks of the trees they were in, were examined. Escape routes may be important not just for protection from predators but in case of attack from other chimpanzees. Only 12 of the 163 nests (7%) did not have an alternative route to the ground. This is further emphasised by the fact that the nearest tree to the nest tree was on average only 2.5m away (range = 0 - 10) measured from trunk to trunk. The second nearest tree was at a mean distance of 4.2m (range = 0 - 11) and the third, 5.5m (range = 0 - 12). If chimpanzees have any concern for protection from leopards, it probably manifests itself by their nesting on branches which enable them to feel a leopard moving onto the nest branch, and by ensuring an adequate escape route through a neighbouring tree. Of the 12 nests without escape routes,

Figure 4. An extraordinarily low nest.

the median height of the lowest branch was only 1m off the ground, so the makers of these nests had apparently made no provision for their safety. An example of an extraordinarily low nest is shown in Figure 3.

5(v).Nest dimensions

Nests at Mt. Assirik were oval in shape and their dimensions tended to be stable across types of vegetation and season (see Table 3). The mean dimensions to the nearest 10cm were 80 x 60cm with a depth of 40cm: ranges were as follows: length 20 - 180cm (N = 157) breadth 20 - 110cm (N = 157) depth 20 - 80cm (N = 155); not all dimensions could be estimated since visibility was occasionally too poor. Only Nissen (1931) and Izawa and Itani (1966) mentioned the shape of nests but in both cases they were oval. Izawa and Itani (1966) gave the average size of a nest as 112 x 89 x 51cm. These measurements were calculated from the nine nests that they examined, but they did not mention if the measurements were taken from the most extreme twigs and leaves of the nests or if they came from measurements of the body of the nest, as ours did. Our figures were estimates, but at the beginning of the nest study estimates were checked against exact measurements and found to be accurate.

At Mt. Assirik, the number of main branches, i.e., those thicker than 2.5 cm. diameter, incorporated into the nest was, on average, only 3 (range = 0 - 7, N = 163). This is fewer than the number of main branches recorded by Izawa and Itani (1966): they found an average of 7 (range = 4 - 10, N = 9). This difference is statistically significant (Median test: χ^2= 7.78, df = 1, $p<0.01$, N = 172), but it may be due to differences in the criterion for a main branch: Izawa and Itani gave no definition.

5.(vi) Other features

Nests were described as either 'open' or 'closed' depending upon whether there was a clear view to the sky directly above the nest, or whether foliage overhung the nest. This feature may be important to the chimpanzee when it rains, since overhead foliage might provide some degree of shelter. It was found from the 160 nests where this feature could be determined that in the

Table 3. Mean dimension of nests by season and habitat.

Season Habitat	DRY	WET
Forest	length 83 cm width 66 cm depth 41 cm N = 51	length 87 cm width 67 cm depth 44 cm N = 22
Woodland	length 80 cm width 62 cm depth 39 cm N = 47	length 78 cm width 57 cm depth 43 cm N = 33
Grassland	length 83 cm width 65 cm depth 42 cm N = 10	

wet season only 16% of nests (9 out of 53) were closed, whereas in the dry season 30% (32 out of 107) of the nests were closed. This apparent seasonal difference was not significant, however (χ^2 test for two independent samples: $\chi^2 = 2.46$. df = 1, $p>0.1$, N = 160).

The largest number of nests found in a single tree was 21, but these were not all of the same age. The tree (Parkia biglobosa) was used for nesting several times during the study period. It was large and spreading, and, situated near the summit plateau of Mt. Assirik, it commanded a fine view. At Mt. Assirik, most forest and woodland occurred on sloping terrain (see mean angles in Ch. 5), so that with the exception of nests made in the forest directly over the streambed, most nests were above slopes and had views of the surrounding land.

The number of nests found which were definitely less than 24 hours old (i.e., of the previous evening) was 367. These were of known age and could therefore be linked with others to assess the size of groups of nests. A nest was included in a group if the distance between it and its nearest neighbour was not greater than the shortest distance between any two nests in the group. Of the 367 fresh nests where number/tree was recorded, the largest number made on the same night in the same tree was 7. Many were made singly in trees (N = 135). The mean was 1.5 (median = 1) and the range, 1 - 7. On one occasion, 16 recent nests were found in the same tree. They all appeared to be of the same age. Elsewhere, 10 is the largest number of nests of the same age found in one tree (Nissen, 1931; Goodall, 1968). Izawa and Itani (1966) found 5 (see Table 1).

6. Nest Groups

The size of the groups of fresh nests varied from between 1 and 18. The mean number of nests at the 83 sites examined between June 1976 and June 1978 was 5.4. This figure is only slightly larger than the mean number of chimpanzees observed together, which was found to be 4.6 (N = 108) in Chapter 6.

Goodall (1965) reported that chimpanzees usually nested in groups of 2 - 6, and that the largest number was 17; whereas Izawa and Itani (1966) reported groups of 1 - 5, with the largest ever found being 9. This latter study, however, was a short one.

At Mt. Assirik, a seasonal difference was found in the size of nest groups. Groups of fresh nests were larger in the wet season than in the dry (Median test: $\chi^2 = 8.92$, df = 1, N = 83, $p<0.01$). The mean size of groups in the wet season was 8.6 (range = 1 - 18, N = 18) and in the dry season, the mean size was 4.6 (range = 1 - 15, N = 65). As there were no seasonal differences in party sizes observed during the day (see Ch. 6) this result suggests that chimpanzees come together in the wet season to nest, but split up during the day to forage. A possible explanation for this is that since chimpanzees are ranging widely during the wet season in outlying, less familiar areas, they tend to move in large parties. This means greater protection from predators and possibly strange chimpanzees, as well as a greater chance of any individual in the party having knowledge of food sources in these strange areas, and leading others to them. Although long-term movements are over a large area, daily movements are only for short distances (as water is readily available). Thus, chimpanzees could safely split up into small foraging parties during the day, maintaining vocal contact and coming together to nest at dusk. Unfortunately, because chimpanzees do range so widely in the wet season and were rarely found, observational data are not available to confirm or refute this hypothesis.

7. Discussion

Nests and nest-making behaviour at Mt. Assirik are remarkably similar to those found in other populations of chimpanzees. The only apparent differences seem to lie in the heights of the nests, the species of trees chosen, and possibly in the sizes of groups of nests, but comparative data are lacking to test this latter feature. In all cases the differences appear to be environmentally determined.

The results showed that the height of a nest is largely governed by the height of the tree. The proportional height at which a nest is built is presumably governed by the proportional height at which the optimum combination of pliable branches and leafy twigs occurs. In any case, the nest is built usually at a level of 0.8 of the height of the tree. The heights of nests varied across the types of vegetation. If the proportional height at which a nest is built remains constant (with the exception of wet season woodland nests), then the height of nests will be governed by the heights of trees in that type of vegetation. This is the case at Mt. Assirik, and it is likely to be the case in other populations of chimpanzees.

Chimpanzees at Mt. Assirik nest in the tallest trees in each type of vegetation. If it is the case in other populations, as suggested by the evidence of Izawa and Itani (1966), then one can ask where chimpanzees draw the upper limit on the height of nests in forests with very tall trees. The evidence of Reynolds and Reynolds (1965) suggests that in the Budongo Forest, where the canopy height is typically 140ft. (43m), few nests (10%) actually occurred over 100ft. (30.5m). Thus there is presumably a point at which nest heights level out. At Mt. Assirik, the vegetation does not allow this; instead chimpanzees nest in the tallest trees available, wherever they happen to be.

Within each type of vegetation, chimpanzees at Mt. Assirik show marked preferences for certain species of tree: these preferences are not related to the relative abundance of the species in the habitat. This has not yet been demonstrated elsewhere. Preferred species seem to be those which are tall, without spines or thorns, and which have a suitable combination of springy branches and abundant soft leaves.

Woodland is the type of vegetation most often used for nesting. This is thought to be because it is the most extensive type of vegetation at Mt. Assirik: this allows chimpanzees to nest in scattered locations. If they were restricted to the forest, which covers less than 3% of the surface area, they would have to nest in the same set of small areas repeatedly. This might attract predators and increase the risk of reinfection by parasites. Woodland may also be preferred because its trees, although not as tall as forest trees, have softer leaves. Grassland is used for nesting, but to a lesser extent than either of the other two types of vegetation. It is used only seasonally (see Ch. 6) while standing water remains. Bamboo areas are not used for nesting: they are hardly used by chimpanzees at all, but the trees seem unsuitable as nest material, e.g., Borassus palms and thorny Acacia trees. Plateaux are not used for nesting because they do not support tall trees (see Ch. 5).

Nesting behaviour in chimpanzees is remarkably uniform. This holds across the three subspecies and within subspecies. Speculation arises as to the evolutionary origins of the behaviour.

Young chimpanzees in the wild have about 5 years of nightly opportunities to watch their mothers building nests before they must make their own. They have ample opportunity to observe and then practise, in play, the necessary skills. If experience is necessary for the full expression of the behaviour, it is surprising that variation in nest-building has not occurred. Its very uniformity suggests that the behaviour was practised before the geographical races of chimpanzees had separated, and possibly before the great apes diverged; all three great apes make similar nests. The only notable difference is that gorillas' nests tend to be low in the vegetation, or on the ground.

The behaviour may have originated in the common ancestor of the great apes, which, with its strong arms, manipulative ability and increased cognitive capacity, discovered the advantages of a comfortable cushion of vegetation. This might first have been made on the ground, for day-time resting; then leafy branches were broken off and laid on top of thick branches in trees. The sturdy nest or platform, with its woven base, developed later. A more comfortable sleep, with greater restorative efficiency, might have been advantageous because it permitted a greater expenditure of energy during the day. Maintaining balance on a branch while asleep, as other primates do, presumably uses up a small amount of energy throughout the night.

The fact that nest-making is so similar across populations of chimpanzees that have long been separated is curious. The only apparent explanation comes from the conservative nature of the chimpanzee. (It is well-known that chimpanzees are reluctant to eat strange foods, e.g., Reynolds and Reynolds, 1965; Kortlandt, 1967). The nests made by chimpanzees are comfortable and functional, and it is hard to imagine an innovation in nest structure which would offer any great advantage. The only useful addition to the nest might be an 'umbrella' - a covering of leaves or branches over the chimpanzee to protect itself from rain. Such 'umbrellas' are sometimes made by orang utans (MacKinnon, 1974; Rijksen, 1978).

It is possible for innovations to occur: the ground nests (13% of total number) found by Kortlandt (1967) suggests that under exceptional circumstances a novel pattern can occur. Elsewhere, however, during the night chimpanzees still run the risk of becoming the prey of nocturnal carnivores, and sleeping off the ground is one measure of protection. The great apes have for a long time been using their skill to build comfortable nests, and, other than altering their location and adding a cover, there has been no reason for them to modify this behaviour.

Chapter 10. CONCLUSIONS

1. Introduction

This chapter aims to draw some conclusions from the natural history of the chimpanzees at Mt. Assirik, as described in the preceding chapters, and ventures to relate them to speculation on the natural history of the early hominoids, i.e., the common ancestors of man and chimpanzee. It then attempts to describe how this may have altered along the hominid line.

In the introduction to this study, chimpanzees were posed to be of value as models for human evolution because of two factors: their close morphological and biochemical relationship to human beings, (e.g., King and Wilson, 1975) and their advanced cognitive abilities (e.g., Premack, 1976). In both respects, chimpanzees are preferable to baboons as models, despite the fact that baboons are well-adapted to life on the savanna. This chapter aims to show how the chimpanzees at Mt. Assirik are particularly important as an evolutionary model because they, too, are well-adapted to the savanna environment in which they dwell.

At least some of the common ancestors of the monkeys, apes and men — the primates of the Oligocene, inhabited an area which experienced alternate wet and dry seasons and which contained belts of riverine forest with intervening areas of open vegetation (Butzer, 1978). Whether the great apes diverged from the hominid line during the Miocene as Napier (1970) suggests, or much more recently, in the Pliocene as Zihlman _et al_.(1978) propose from biochemical analyses, is still a matter of debate. What concerns us here is the important new finding that their common ancestors lived in areas of mixed types of vegetation, and that hominoids of the Miocene and Plio-Pleistocene continued to exist in these mosaic habitats (Butzer, 1978). All this suggests that discussion of the evolution of man in terms of his moving out of the dense forest onto the open plains (e.g., Zihlman and Tanner, 1978) should be reconsidered: the ancestors of man, as far back as his common ancestor with the great apes in the

Oligocene, dwelt in mixed, partly open habitats. From that point onwards, hominoids and hominids continued to inhabit these areas. Thus, among the primates, it was largely the monkeys and apes which must have changed habitats, by moving into the areas of dense forest.

At some point, the pongids diverged from the hominid line and eventually became more specialised for their forest existence. Chimpanzees at Mt. Assirik today dwell in a savanna environment which is not typical of their species; but it is typical of the one in which the hominids evolved. By examining the way in which these unusual chimpanzees are adapted to their environment, as opposed to chimpanzees in more wooded areas, we can propose hypotheses concerning the adaptive strategies of the ancestral hominoids.

As a further source of information, we can draw on a more highly developed group of extant hominids, living in an environment which is similar to that of the ancestral hominoids. These are modern men practising the simplest patterns of subsistence, in seasonal habitats in Sub-Saharan Africa. I refer to living hunter-gatherers, who, without agriculture, and extensive preservation and storage of food, represent the most basic form of human subsistence that exists today. The best-documented hunter-gatherers are the San, who live in arid areas of Botswana. They have been the subjects of extensive, systematic study since 1963 (Lee and DeVore, 1976).

By drawing attention to two populations of extant hominoids, this chapter does not attempt to conclude that behaviours which are common to both species must have been behaviours practised by their common ancestors. Instead, it accepts that both species are phylogenetically closely related and have cognitive capacities which are not qualitatively, but only quantitatively different. It attempts to examine how similar their environments are to the environment of the earliest hominoids. Where similarities are found, the appropriate behavioural adaptations of living hominoids are used as a basis for speculation on the behaviour of their ancestors. The development of the hominid line will be proposed on the basis of the gap between this speculative reconstruction and the ecology of living hunter-gatherers.

Sound bases for speculation are desirable because many important aspects of the behaviour of ancestral hominoids have left no trace. Whereas later hominids left stone tools (Clark, 1976) as evidence of an important aspect of their adaptation, it is likely that the first tools made were of vegetation and could have been made by early hominoids, since wild chimpanzees make a small variety of such tools (see Ch.8: Goodall, 1968, Nishida, 1972). These implements disintegrate and leave no evidence. Diets cannot be described unless food remains are found; where animal bones are discovered, with evidence that they have been prepared for eating we can infer which species provided meat in the diet, but plant remains are rare. This means a definite bias towards animal foods in the interpretation of diets of the hominids. The examination of coprolites would overcome this problem, as well as providing a means of direct comparison with living hominoids (e.g., Heizer and Napton, 1969) but such analysis has not been carried out extensively. Finally, aspects of social organisation, perhaps the most complex feature of our evolutionary inheritance, are almost impossible to deduce from any kind of fossil evidence, so that any well-founded hypotheses on this score are both useful and interesting.

The discussion will be roughly divided into three parts: habitat; subsistence; and social behaviour. In the first section, environmental similarities are described with the implications that they might have for ranging patterns and the composition of groups. In the description of subsistence, its influence on the development of food-sharing and social relationships is suggested: in the last part, an aspect of the social behaviour of chimpanzees at Mt. Assirik is proposed to have a bearing on the development of sexual relationships. This chapter is not presented as a definitive outline of the evolution of the hominids, but merely as a demonstration of ideas which have been suggested by the natural history of these special chimpanzees at Mt. Assirik.

2. Habitat

As mentioned earlier, recent evidence shows that the first hominoids dwelt in areas of mixed types of vegetation, with patches of gallery forest interspersed with more open areas. This continued to be the case apparently for all early hominids (Butzer, 1978). With reference to vegetation, their habitat more closely resembles that of chimpanzees at Mt. Assirik than of the San, whose environment is drier and seems to be more uniform in its openness: tree and bush savanna (Yellen and Lee, 1976) without strips of gallery forest. Rainfall there is seasonal, and about half that at Mt. Assirik: it also shows considerable inter-annual variation, as does Mt. Assirik (Ch. 3). Presumably these factors give rise to the sparse vegetation.

Research into the geo-ecology of early hominoids and hominids can tell us about the climate that prevailed during those times. Although annual rainfall seems to have varied in the early Miocene, it was about 1000mm per annum, similar to Mt. Assirik. This seems to have remained roughly constant through the Miocene, but with greatly increasing local variation as a result of rift-fracturing and topographic diversity. The habitats all appear to have been highly seasonal with respect to rainfall, with evidence of periodic flooding and leaching of the soil (Butzer, 1978).

Thus all three habitats show climatic variation, with a marked seasonality in the rainfall. The most important effect of this for chimpanzees at Mt. Assirik, and for some of the San communities, is in the amount of residual drinking water at the end of the dry season. Chimpanzees spend more time in the forest at the end of the dry season than in any other type of vegetation (Ch. 6) and this seems to be because of the need for water, rather than a result of the distribution of food, since food is available elsewhere at that time (Ch. 8), whereas water is not. For the San, daily movements to gather food are restricted to a much smaller area surrounding a water-hole in the dry season than at other times of the year (Yellen and Lee, 1976). This is because gatherers are reluctant to carry the necessary quantities of water for long distances.

For the early hominoids, if water was scarce during the dry season, home ranges or settlements might have been made near the remaining streams or pools of water. Evidence of the location of both hominoid and hominid remains supports this (Butzer, 1978). A later development in the location of hominid home bases might have been to make settlements near, but not directly beside water. The San do this in order not to disturb animals that come to drink at the water-hole, since these are a potential source of food (Yellen, 1976). Before regular hunting of game, hominoids might have spent the night close to water, but with the advent of regular hunting for larger prey, e.g., adult ungulates, they may have begun to make night settlements some distance away. This would also have decreased the risk of reinfection by parasites, since defecation would take place further away from the source of drinking water.

The fauna existing at Mt. Assirik and coexisting with the San are similar with respect to large carnivores and the variety of ungulates (Ch. 3; Tanaka, 1976). Primates are lacking for the San, however, presumably because there is insufficient water.

Evidence from two early Miocene sites where hominoid fossils have been found, indicate greatest diversity among the herbivores and carnivores. Ten species of primates have been discovered at each site (Van Couvering and Van Couvering, 1976): six species of Pongidae and four species of Lorisidae. The latter are arboreal primates (Napier, 1970) and must have been restricted to the areas of forest. The former may well have competed with one another in the more open areas and the successful species were probably the most versatile: those which had the ability to use several types of vegetation, with appropriate seasonal adaptation. This would have been especially important with inter-annual variation in rainfall. This strategy is employed by chimpanzees at Mt. Assirik. They coexist with two species of Lorisidae and three species of diurnal Cercopithecidae. These latter three species each make use of more than one type of vegetation: green monkeys use forest and woodland primarily; patas monkeys generally keep to the most open land, plateaux and the fringes of the woodland; baboons use all types of vegetation.

For the San, the threat of large carnivores seems to be overcome by their keeping in groups whenever they gather or hunt. By this method they will not be attacked by large carnivores, which might prey on single persons (Yellen and Lee, 1976). Similar conditions may hold for chimpanzees at Mt. Assirik: single individuals when away from the trees of the forest or woodland, could be vulnerable to attack; but a group with more than one adult, preferably with at least one adult male, is thought to be safe from predators. The most common social grouping for the chimpanzees is the mixed group. This suggests that weapons are not required for self- defence on the savanna, but either access to trees, or movement and settlement in mixed groups is necessary for the safety of the great apes, modern man and possibly early hominoids. The early hominoids coexisted with felids (Van Couvering and Van Couvering, 1976) but given the examples above, it seems unlikely that early tool use developed first as a means of making weapons for self-defence.

3. Subsistence

Until recently, the hunting and eating of meat was considered to be one of the major influences on the development of man's culture and social organisation: the first use of tools as weapons; the development of language; pair-bonding (Washburn and Lancaster, 1968). Recent research, e.g. Lee and DeVore (1976) has pointed out that modern hunter-gatherers in the tropics and subtropics subsist mainly on the products of gathering and not from hunting. Plant food forms the bulk of their diet, and meat is a more highly prized item, taken where possible, but not to be depended upon. Thus, the sets of behaviour associated with the social organisation and culture of the early hominoids should be considered for their relation to a gathering, omnivorous way of life.

Chimpanzees at Mt. Assirik are omnivorous but depend on plant foods to subsist. Some insects are eaten seasonally; others, along with meat and honey, appear to be taken opportunistically. San hunter-gatherers are also omnivorous but depend mainly on plant food: beans, berries and tubers. Migrations are determined by the availability of water in northern groups of San, and by the availability of plant foods (the only source of water at the end of the dry season) in southern groups. In neither case are seasonal movements determined by the availability of game. These two groups of extant hominoids range according to the availability of water, indirectly or directly: in a seasonal African savanna habitat, the early hominoids probably did the same.

One very important difference between today's San and the chimpanzees at Mt. Assirik chimpanzees lies in the regular carrying and sharing of food. This is a fundamental fact of life in the San: it does not occur in the chimpanzees. How the systematic carrying and sharing of food came about can be postulated by beginning with the existing patterns of food-sharing among wild chimpanzees.

Chimpanzees at Mt. Assirik eat meat, but as far as we know, they eat only nocturnal prosimians (Ch. 8) which remain hidden in nests during daylight hours. Catching and killing probably depends on the opportunistic discovery of a nest and does not involve the pursuit of prey: it seems likely that males and females are equally adept at this. Where the pursuit of prey is involved, however, as at Gombe, sex differences do exist (McGrew, 1979); it is predominantly adult males which hunt. Males sometimes share meat with other individuals. The important difference between this sharing and the meat-eating among the San for example, is that in chimpanzees the sharing is generally not displaced in time or place from the actual kill.

From Gombe we also know that adult female chimpanzees share plant foods with their offspring (Silk, 1978) and sometimes among other kin (McGrew, 1975).

A plausible hypothesis for the development of extensive carrying and sharing food is proposed thus: Among the early hominoids in the more open areas of mixed vegetation, males, females and young travelled and foraged together as a mixed group, subsisting mainly on plant food with the occasional opportunistic killing of small or immature mammals. (This habitat and pattern of subsistence is that of the Mt. Assirik chimpanzee). Occasionally males gave some of the highly prized meat to females, after they had satiated themselves. Such generosity may have been an influential factor in the preferences shown by female chimpanzees for mating partners when in oestrus. Females shared plant foods with their offspring, often in response to begging. Females began to share plant food occasionally with males, to increase the probability that a male would give surplus meat in return when he next made a kill. At this point the supposed path of early hominoids deviates from behaviour shown by chimpanzees. The reciprocal giving of food began to occur not at the same time, but was delayed. At this point tools were mainly used for the gathering of plant foods, e.g. smashing hard-shelled nuts as chimpanzees can do (Struhsaker and Hunkeler, 1971; Rahm, 1971) and grinding, as the San do (Yellen and Lee, 1976); gathering insects (Ch. 8); unearthing underground bulbs and tubers, or subterranean rodents, with a digging stick, as the San do (Tanaka, 1976). The use of tools later extended to be used for the killing and butchering of large game, at first as simple forms with one component, or facilities (Oswalt, 1973) such as grass knots for tripping game. Males began to spend more time hunting, where their greater strength, agility and throwing propensity (see Goodall, 1968, for male chimpanzees' throwing tendency) gave them more success than females. As males spent extended periods in the pursuit of meat, a highly-prized food, females and offspring foraged without their protection. When venturing out onto expanses of grassland for example, it became more advantageous for females to leave weaned but immature offspring for short periods in the care of older siblings or grandmothers. (San children, after being weaned do not accompany foraging groups until after adolescence; Draper, 1976). Those left behind remained in the safer, cooler forested or wooded areas until adult females returned with small amounts of gathered plant food and shared it amongst them. (Wild chimpanzees in Guinea carry human crops away from the open fields to the fringes of the woodland, Albrecht and Dunnett, 1971). Males still usually relied upon the plant food which they gathered and ate on the spot. Meat was also eaten at the site of the kill, but surplus food was carried for a while and eaten later, or given to those who begged for it. Males and females still sometimes foraged together, and the meat was shared when parties joined together again. On occasions when males had spent long periods in the pursuit of prey and had not eaten sufficient complimentary plant food, or when they rejoined females after an unsuccessful hunt, they begged and received plant foods from females, since the females by then were regular collectors and donors of food.

The female most likely to give plant food to a male was the one to whom he had given meat in the past. Differences in the proportions of types of food gathered by each sex became more pronounced. Females left young in the care of close kin for longer and longer periods, and accordingly they had to increase the amount of food which they carried back. Males could afford to spend more time in the risky pursuit of game, relying on begged left-over food from females, in reciprocation of the rarer, but more highly-prized meat which they gave. Upright posture may well have developed from the more frequent dragging of dead animals (as prey became larger with the development of tools) or branches of fruit, or the carrying of food away from the open areas to the cover of trees where they could be consumed more safely and where sharing took place. Bipedal walking would also have been useful when tools or artifacts were carried for re-use, and the container (e.g., hard fruit cases or empty egg-shells) was invented.

Nomadism continued to make the best use of the seasonal environment, but daily movements between nesting or camping sites became smaller in distance, or sites were only changed every few days, since surplus gathered food would be eaten before a party moved on. Party sizes were variable, according to the distribution of water and plant food (this occurs in the San today, Lee, 1976) and in chimpanzees (Ch. 6; Wrangham, 1975). The meeting points for the exchange of foods were at first determined by calls, extensions of the calls given to signal a source of abundant food to another foraging party. This occurs in chimpanzees (Wrangham, 1975). Later when temporary camps lasted longer, food calls were abandoned. The use of a spoken language developed from the complex cognitive abilities and gestural repertoire which were needed to pass on information about the environment, and to pass on cultural knowledge on the use of tools to gather and process food, the spatial arrangements for gathering and hunting parties, the cooperative use of facilities, e.g., the setting of snares and driving game. The spoken language developed when the social, cultural, and use of the physical environment became too complex for the gestural mode; and when mere observation, with trial and error learning during childhood was too time-consuming for the assimilation of useful knowledge in a lifetime. The gestural mode is highly developed in the chimpanzee (Plooij, 1978) which also has the capacity for a verbal language (Premack, 1976), presumably because the chimpanzees use of the environment, their social organisation and use of tools represent a complex way of life.

The manufacture and use of tools deserves special mention. Subsistence technology varies enormously across human populations, even among the few remaining hunter-gatherer cultures. It also varies across chimpanzee populations, but as far as we know, to a much lesser extent. Adult chimpanzees are essentially conservative creatures: it is the young which are playful and exploratory and which imitate readily (e.g., Goodall, 1975). In the wild, young chimpanzees are most likely to imitate adults, particularly their mothers, with whom they spend most time. Thus, existing customs are passed on from adults to offspring, but innovations by the youth are unlikely to be adopted by the conservative adults. This is offered as a possible explanation of why chimpanzees, at Mt. Assirik, for example, which live in an environment similar to that of our ancestors, have not developed an array of tools to facilitate their subsistence. Specific examples of useful tools would be hammer stones and anvils to smash open the pods of Afzelia africana. The seeds inside are eaten but are inaccessible for several months when the pod is too hard to open (Ch. 8). The young chimpanzees of the rehabilitation project have been successfully shown how to do this, and other populations of wild Pan t. verus use such a technique (Struhsaker and Hunkeler, 1971; Rahm, 1971). Digging sticks could be used to dig up or dislodge bulbs and tubers as local people do (pers. obs.). Poking sticks could be used to flush out bush-babies and pottos during the day. We once observed an adolescent wild chimpanzee strip several thick sticks of leaves and then poke them vigorously into a large hole in a dead tree. Upon later inspection, we could see nothing in the hole, in particular no insects. It may be that such a practice is used by chimpanzees when searching likely-looking holes of bush babies and pottos, as is the case with local people. Nishida (1973) described one incident of almost identical behaviour among chimpanzees of the Mahali Mountains, the only other population known to eat bush babies, (Nishida et al,, 1979). Although no ants were found on the dead branch, he attributed this incident to the chimpanzee's attempt to expel insects from the hole. Since the capture of a galago has not been seen there, it is possible that the "expelling stick" (Nishida, 1973) is sometimes used for this purpose. Crumpled leaves as sponges would be especially useful to exploit residual water in tree hollows; these are used at Gombe (Goodall, 1968).

Perhaps an important development in the early hominoids came when extensive food-sharing began: more stable, close bonds among kin and preferred partners meant that there was a higher probability of imitation beyond the young chimpanzee's imitation of adults. This meant that innovations could be extended throughout a single party, then community, and then to a neighbouring community when individuals, most likely adolescent females (Nishida and Kawanaka, 1972; Pusey, 1979) migrated to them.

4. Social behaviour

Social behaviour and organisation could not be described in detail in this study: the most interesting finding was the prevalence of mixed parties as opposed to parties of any other composition (see Ch. 7). The simplest explanation for this is that it is an adaptation to the fauna coexisting at Mt. Assirik. It is unlikely that chimpanzees in parties containing one or more adult males will be attacked by large carnivores when ungulates are much more common in the area (see Ch. 3) but an adult female, carrying an infant, and with a juvenile following behind, would seem to be easier prey when away from the safety of the trees. The increased frequency of mixed parties compared with other populations of chimpanzees (see Ch. 7) may be an adaptation that early hominoids made before any extensive food-sharing or pair-bonding occurred. It would be fascinating to know if adult males at Mt. Assirik frequently change mother and offspring parties, or if they tend to spend long periods with the same matrilineal kin group. It seems likely that they change frequently, given the apparently universal fluidity of social groupings in chimpanzees; but even so, the opportunities for affiliative bonds to arise between males and females are greater than among other communities. This has important implications for the mating strategies of adult males.

If at Mt. Assirik, males more frequently accompany adult females and their offspring, the opportunities for giving attention to a particular female and her offspring are greater and may increase the probability of her favouring him when she next becomes fertile. As far as sexual behaviour is concerned, the advantages of being an alpha male would be decreased, except when party sizes are large and several adult males are competing for an oestrous female. Similarly the rate of opportunistic mating which occurs when large parties containing an oestrous female are formed, is reduced; most conceptions would result from a preferred male's exclusive access to a female: he would reap the benefit of his investments of attention. It follows that many of the mixed parties observed, i.e., those containing only one adult male, are in effect consort parties, whether the female is fertile or not.

This hypothesised trend among chimpanzees at Mt. Assirik, presumably stemming from their adaptation to potential predators, may well have been one which developed in the hominoids. It thus represents a transitional system, i.e., a phase between a social system with several adult males in frequent, direct competition for fertile females, and the pattern of serial monogamy which exists in the San (Howell, 1976) and is widespread in human cultures. The closer, extended contact between adult males and females conforms with the development of patterns of meat and plant food sharing outlined earlier.

5. The natural history of chimpanzees at Mt. Assirik: implications for the future.

First of all, it appears that the population of chimpanzees at Mt. Assirik is stable: at least, there were no age classes out of proportion nor an abnormal sex ratio in adults (see Ch. 7). No illness or evidence of infectious disease was apparent. There is a low probability of their contracting human disease since no resident human populations exist in the park and contact between researchers and chimpanzees is minimal. Any seriously ailing chimpanzees probably have little chance of survival, because of the need to travel large distances for food and water: stragglers leaving forested areas may be the victims of one of the large carnivores.

At the moment, little can be said of the competition with baboons in the area. This may well be a limiting factor on growth in the population of chimpanzees. A single group of over 600 baboons was once observed near one of the small strips of gallery forest in the chimpanzees' home range (Sharman, pers. comm.). Groups, varying in size from about 30 to 300, regularly spend the night in Lion Valley, and on the same nights baboons are sleeping in other patches of gallery forest within the chimpanzees' range. Some elements in the diet differ, e.g., baboons eat a variety of bulbs and seeds which chimpanzees do not, but many fruits are common elements to both diets: moreover, baboons seem to eat some fruits at an earlier stage of ripeness than chimpanzees. Some species of fruit are eaten by all four diurnal primates in the area, e.g. Strychnos sp. The high density of baboons indicates that they are perhaps the best adapted of the four primate species, for they feed in all types of vegetation.

The chimpanzees probably survive at Mt. Assirik in a delicate balance with the resources of water and food (the distribution rather than quantity) and with the baboons in competition for the food. A drought might reduce the small population of chimpanzees to a size which is untenable: given the inter-annual variation known to occur in West Africa (Winstanley, 1978) this is a possibility. Similarly, a rise in the population of baboons might also reduce their numbers. Just how fine the balance is between chimpanzees and baboons remains to be seen from current studies.

Green monkeys and patas monkeys are not considered to be major competitors: both species eat some plant foods in common with chimpanzees, but the populations are smaller than that of the baboons. Their body weights are smaller and their ranging either more specialised, avoiding areas used by chimpanzees, in the case of patas monkeys, or much smaller, in the case of green monkeys.

The key to the chimpanzees' survival seems to be their massive areas of home range, their seasonal adaptation to the resources, and probably their omnivorousness. The flexible social system is probably an advantage in a variable habitat: Mt. Assirik is one of the most variable chimpanzee habitats existing.

It is not known how long chimpanzees have existed at Mt. Assirik and therefore they may be living an untested and precarious life on the fringes of the species' distribution. Assuming their continued protection within the park, care must be taken not to upset the delicate balance in which they live. An influx of tourists, or the installation of a large, permanent guards' post at Mt. Assirik, with the resultant, heavy traffic, might just be enough to reduce the population to a critically low level by making part of their range unusable, or cause them to move south across the Gambia river (if that is their origin). The attacks in 1978 by wild chimpanzees on the rehabilitation project's free-ranging chimpanzees, may be a response to some unknown, but critical increase in pressure on their resources.

There does not seem to be a limit to the amount of useful knowledge that can be gained from studying a population of wild chimpanzees. After 19 years of continuous, close-range observation of chimpanzees in the Gombe National Park, by numerous researchers, fascinating findings are still emerging (Goodall _et al_., 1979). Such a complex species as the chimpanzee remains to be understood. Studies can be justified on the basis of their bearing on the explanations of human evolution, but they are equally justifiable on the basis of our ignorance of aspects of their behaviour in many habitats. Wild chimpanzees are disappearing, and wild chimpanzees in a truly natural environment are now rare: as much information as possible should be gleaned from them, throughout their distribution, before they vanish.

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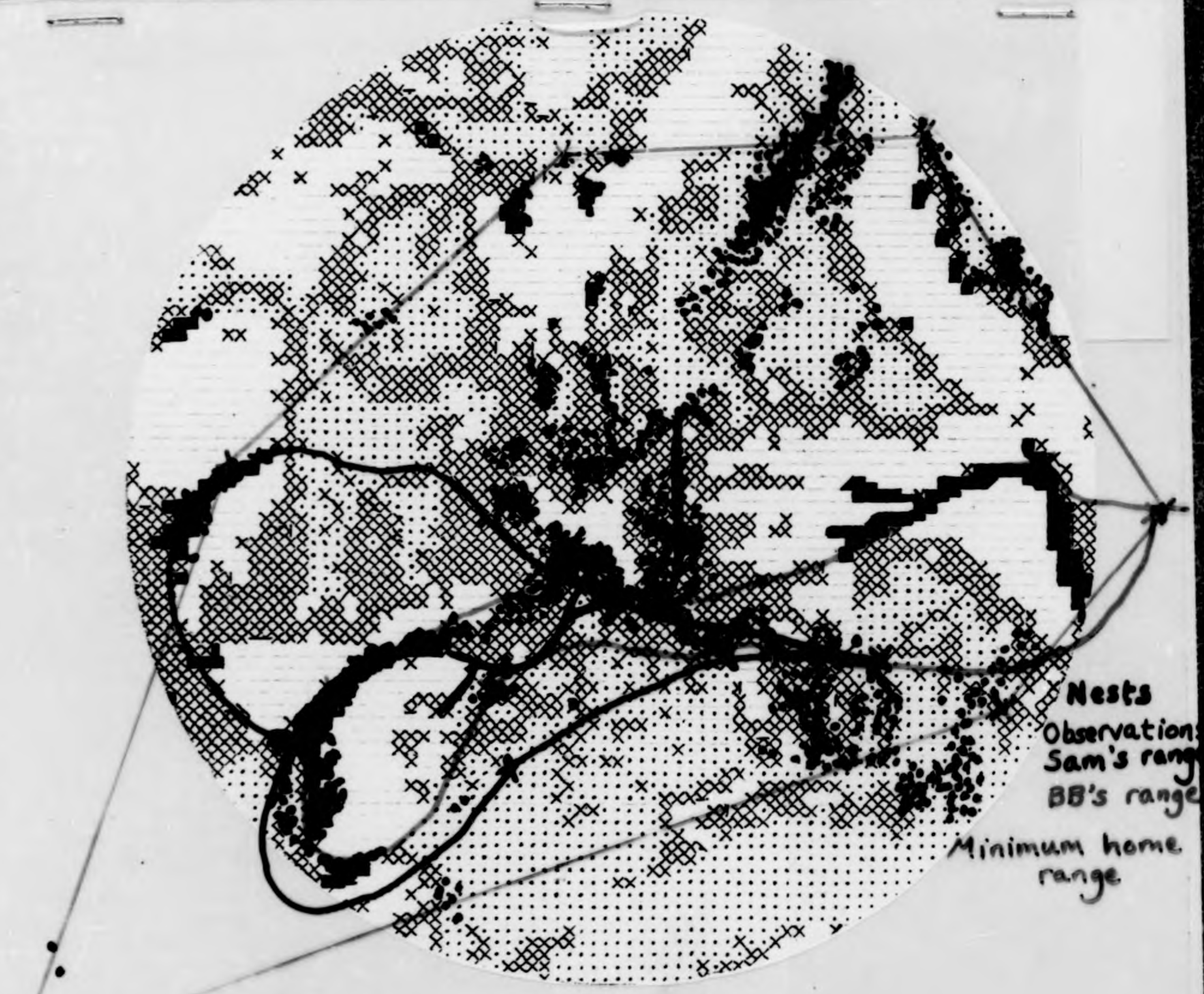
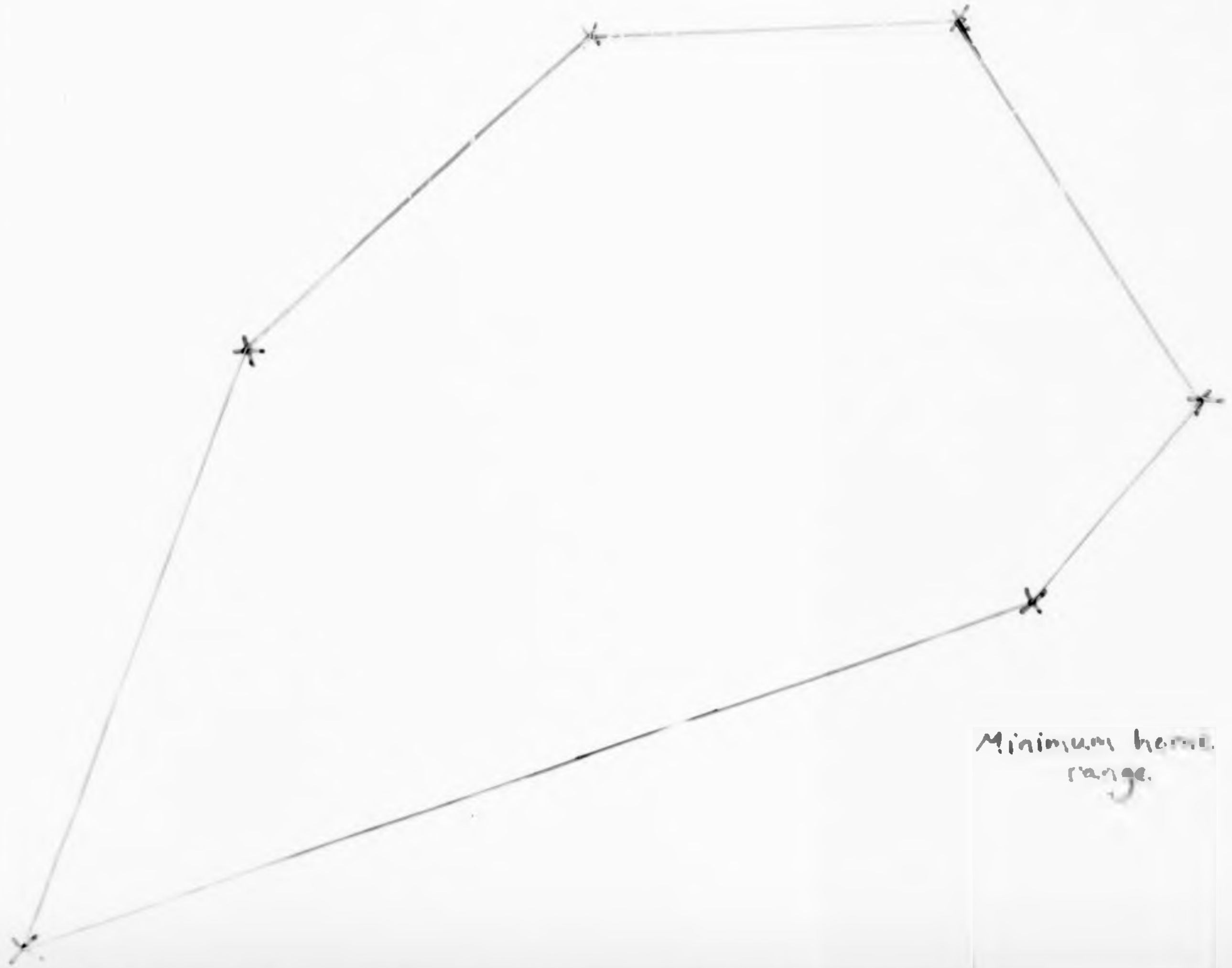
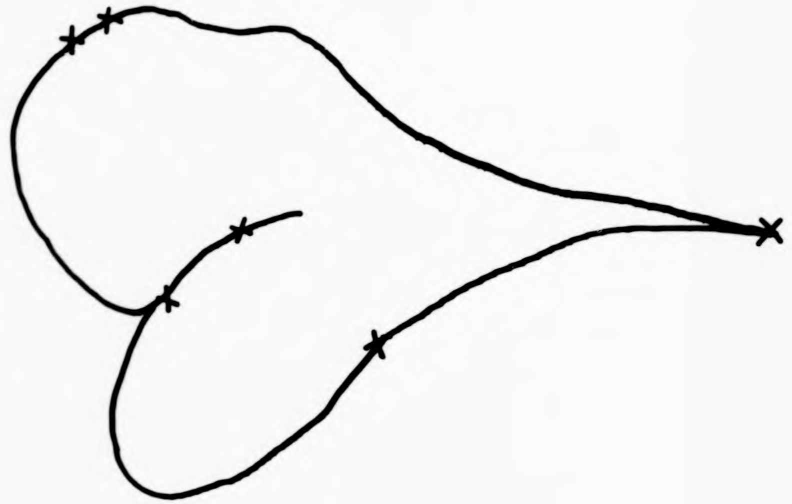


Figure 4. The accumulation of data used to estimate minimum home range.



Minimum home range.

BB's range



Sam's range


Observations


Nests

Figure 4. The accumulation of data used to estimate minimum home range.

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END