The Comparative Ecology of Blue Monkeys (*Cercopithecus mitis stuhlmannii*) in Logged and Unlogged Forest, Budongo Forest Reserve, Uganda: the effects of logging on habitat and population density.

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Declaration

I hereby declare that this thesis was composed by my own hand and that all analyses and data presentation were carried out by me. The data were collected in the field by myself and Geresomu Muhumuza, except data made available by A.J.Plumptre, as stated in the text.

ABSTRACT

Selective timber harvesting in tropical rain forests is becoming increasingly common and plays an important role in integrating economic development needs and conservation goals. Understanding the effects of logging on forest ecosystems can contribute to the design of sustainable management techniques and minimise the negative effects of timber harvesting on wildlife. Despite this, few previous studies have attempted a detailed ecological investigation of the effects of logging on wildlife.

Here I present the results of a comparative study carried out in logged and unlogged forest in the Budongo Forest Reserve (January 1993 - September 1994) investigating differences in blue monkey (*Cercopithecus mitis stuhlmanni*) ecology and habitat composition. The ecology of groups of blue monkeys in logged and unlogged forest was compared and attempts made to relate differences in ecology to differences in habitat composition and food availability. In Budongo, widespread selective felling of 'mahogany' (genus *Khaya* and *Entandrophragma*) over the last 60 years has had a considerable impact on the plant and animal communities, resulting in significant changes in vegetation communities and an increase in density of four primate species (Plumptre et al 1994).

It is thought that unlogged forest tends towards a low species diversity (monodominant) forest type, with *Cynometra alexandri* as the dominant tree species. In addition, logging in Budongo has typically been carried out at a relatively low intensity. These two factors have been important in determining the nature of the changes in vegetation composition and plant phenological patterns subsequent to logging. Noticeable among these differences are a higher tree species diversity and higher proportion of colonising tree species in logged forest relative to unlogged forest. As a result, blue monkeys in Budongo experience greater food availability, occupy smaller home ranges and attain a higher population density in logged forest.

There are several considerations which are important when discussing the findings of this study in the context of forest management for timber production. Firstly, the unique nature of the vegetation in Budongo prior to logging, and the type of timber harvesting carried out, both play an important role in determining the response of the vegetation and wildlife communities. Secondly, although logging in Budongo may lead to an increase in the density of blue monkeys and other common generalist/frugivore species, it may have negative effects on other more ecologically specialised taxa. The findings of this study are discussed in the context of understanding the effects of management on the vegetation composition and blue monkey density in the Budongo Forest Reserve.

The results support the observation that the effects of logging are complex and in some cases can even be beneficial to wildlife. Forest management should take into account prior knowledge of forest types and the likely response of wildlife communities. If tropical foresters are to satisfy economic development requirements and meet conservation goals then management must be applied with care and after some consideration of the potential effects on the ecosystem.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

Tropical rainforests throughout the world are simultaneously experiencing increasing rates of deforestation/degradation, and increasing attention as important areas for the conservation of biodiversity. Deforestation and degradation occur at a range of rates and intensities throughout the tropics driven by factors both socio-economic and political (Buschbacher 1990, Longman 1987, Uhl et al 1991, Wilkie et al. 1992). At the same time there are increasing attempts to conserve biodiversity in these forests, and a relatively large amount of funding is being made available for that specific purpose (IUCN/UNEP/WWF 1991).

One potentially sustainable way to manage tropical rainforests for economic and conservation purposes is to remove timber selectively (Buschbacher 1990). The all too apparent dangers of selective felling, if carried out on an unsustainable basis, are the serious degradation of the eco-system, followed by species extinction or total loss of forest cover (Whitmore and Sayer 1992). However if sustainable selective felling can be carried out, especially where forests are unavoidably scheduled to be logged, opportunities exist to manage timber and biological resources sustainably (Grieser Johns and Grieser Johns 1995). Sustainable selective felling can only be arrived at if a broad understanding of effects on forest structure and wildlife are known. It is therefore becoming increasingly important to understand the effects of management on the ecological systems and individual species which exist in the remaining areas of tropical rainforest (Howard 1991, Johns 1992).

A variety of felling systems and management practices exist and are applied in different rainforests and in different circumstances [see Buschbacher (1990) for a review]. They range from intense, almost clear-cut felling (Cannon et al. 1994) to strip felling (e.g. Palcazu Valley, Peru: Hartshorn and Pariona 1993) and very selective removal of timber by non-mechanical means (Struhsaker 1987). Recent approaches to sustainable harvesting attempt to mimic natural disturbances (for example wind throw or lightning strikes) as closely as possible and by doing so arrive at a sustainable management system (Brown and Press 1992, Skorupa and

Kasenene 1987). Whether any system thus far employed is sustainable is a matter of some debate (Brown and Press 1992, Johns 1992, Uhl et al 1991). Factors as diverse as timber density, economic value of timber, political climate and ecosystem stability can all influence the nature and extent of the management approach. In most cases, the circumstances in which felling is carried out are unique to the specific forest; therefore it is difficult to predict the effects of management.

Understanding the Effects of Logging.

Despite considerable work investigating silvicultural practices in relation to forest management and the effects of felling on vegetation structure, understanding the responses of wildlife to felling and changes in forest composition remained an area of research much neglected. More recently however, as our awareness of the importance of conserving rainforest biodiversity increases, studies attempting to make detailed investigations into the effects of logging on rainforest wildlife have become more widespread (see Johns 1992 for a review). For the purpose of this discussion, the effects of logging on forest ecosystems can be broadly classified as either abiotic or biotic. Abiotic effects, which will not be discussed in detail here, include: changes in soil conditions (carbon content, nutrient levels etc.); changes in climate and hydrology (see Anderson and Spencer 1991 for a review); and indeed economic and sociological changes (Johns 1988b, Uhl et al 1991, Wilkie et al 1992).

The biotic effects of logging on forests are primarily changes in vegetation structure and composition (Cannon et al 1994, Johns 1988a, Kartawinata 1978, White 1992, 1994a). Changes in spatial and temporal patterns of phenological production may also be observed in certain circumstances (Johns 1988a, White 1994c). In addition, changes in population density and ecology of mammals (Nummelin 1990, Plumptre et al. 1994, White 1992), birds (Owiunji unpubl. data, Thiollay 1992) and invertebrates (Kasenene 1984, Nummelin 1991) have been reported from several sites. Although the number of studies investigating the biotic effects of logging are relatively few, some predictors of response have been identified (Johns 1992, Skorupa 1988, 1986). Most of these observations are based on logging intensities, ecosystems and post-logging conditions which are very site specific and therefore should be considered as individual cases rather than widely applicable examples.

Within this body of research, primates are one of the few taxa which have been studied reasonably well. Their contribution to the total biomass, their importance in the ecosystem as frugivores/dispersal agents, and the ease with which they are observed have been the main factors resulting in the depth of study on this one taxon. In addition, some primate species may be important indicators of forest health (Oates 1986) although the validity of this observation has been recently questioned (Plumptre and Reynolds 1994). As a result of this focus on primates, there is a growing body of literature comparing population densities and ecology in logged and unlogged areas of forest (Grieser Johns and Grieser Johns 1995, Plumptre and Reynolds 1994, Skorupa 1988, Weisenseel et al 1993, White 1992, 1994). Specifically, the responses of primates have been characterised by changes in activity budgets, dietary composition, group structure and demography (Johns 1981, 1985b, Skorupa 1986). Classifying species on their dietary and ecological flexibility has been suggested as one way of predicting responses (Skorupa 1986, Johns 1992), and it is generally thought that more ecologically specialised species are more likely to be adversely affected.

Some problems are encountered due to the methodological difficulties of conducting 'before and after logging' studies, and indeed the long periods required for investigating the effects of forest management on ecosystems. In some cases (e.g. this study) post hoc logging studies can provide an opportunity to compare logged and unlogged forest areas in a short term research period. This method makes the basic assumption that the two sites were similar in terms of vegetation composition, soils, climate and mammal densities prior to logging.

The Case Of Logging In Uganda.

Loss of forest cover in Uganda over the last 100 years has been no different in rate and extent from many other African countries (Struhsaker 1981, World Resources Institute 1988). Deforestation in Uganda due to forest clearance for agriculture has been recorded as early as 5,000 years BP. and has continued up to the present (Hamilton 1984,1986). Timber extraction has been carried out throughout the 20th century and has resulted in most of Uganda's Forest Reserves being logged to some extent (Howard 1991). The remaining forest cover therefore consists mainly of disturbed or secondary forest with small areas of protected natural forest present in a system of Nature Reserves. At present total forest cover amounts to around 3% of Uganda's land surface and is being lost at an estimated rate of 2% per annum (Struhsaker 1987). Demands for timber, fuelwood and agricultural land are increasing (Tabor et al. 1990, Struhsaker 1987) and like many other African nations, Uganda is in the process of developing its economy and infrastructure. Given the market value of timber at present, harvesting of mahogany presents an opportunity to make use of the remaining forest areas to generate income. However there is also an increasing awareness that the bio-diversity of the forest ecosystems should be conserved (Howard 1991) and attempts are being made to ensure that timber harvesting from the country's remaining forests is sustainable. Uganda is therefore in the process of integrating timber harvesting and conservation of forest biodiversity in its remaining Forest Reserves. In addition to helping design better systems of management, investigating the effects of logging can help understand the ecological value of 'secondary' or logged forests (Brown and Press 1992, Grieser Johns and Grieser Johns 1995). Howard (1991), in his recommendations for research aimed at improving management in Ugandan Forest Reserves, listed research into the impact of logging on wildlife communities as one of the priorities. As well as a program to increase the size of the Nature Reserve system within the Forest Reserves, continuing research into the effects of timber harvesting on the ecosystem is therefore a vital part in achieving that goal (Tabor et al. 1990).

Rationale For This Study.

Despite the fact that a growing number of studies have investigated the relationship between logging and primate densities, few have investigated in detail the ecological response of primates in terms of diet, ranging patterns and social organisation (but see Johns 1981, 1986, 1988a). Evidence that primate densities in logged (and 'disturbed') forest are often higher than those in similar but unlogged (or 'undisturbed') forests is growing (Fimbel 1994, Grieser Johns and Grieser Johns 1995, Pinto et al. 1993, Plumptre and Reynolds 1994). In the context of this observation, it is important to understand the factors responsible for the higher densities and to incorporate such knowledge into forest management systems.

Preliminary findings of census work in the Budongo Forest Reserve indicated that primate densities were higher in all compartments of logged forest as compared to unlogged forest (Plumptre et al 1994). These differences were highly significant for three out of five species of primate but the exact processes causing these density increases were not known. This study was therefore undertaken to investigate what, if any, ecological differences were observed between groups of blue monkeys (*Cercopithecus mitis stuhlmanni*) in logged and unlogged forest and if such differences were important in determining blue monkey density. In Budongo, blue monkeys in neighbouring areas of forest exhibited distinct differences in density and were relatively easy to habituate to the level required for collection of detailed ecological information. In addition, there is a large body of comparative information detailing the ecology of the *C.mitis* group in a range of sites where previously studied. It was thought that an investigation of blue monkey ecological adaptations in relation to vegetation differences in logged and unlogged forest would allow the testing of the following hypotheses regarding the effects of logging:

1.2 HYPOTHESES

The first hypothesis being tested is that logging in undisturbed forest has resulted in significant long term changes in vegetation structure and composition. A comparison of tree species diversity and relative abundance is likely to reveal differences 45 years after logging. Vegetation structure, abundance and distribution of important food tree species and habitat heterogeneity may also differ between the two areas. In addition to differences in species composition and abundance, differences are also predicted in patterns of seasonal plant part production. Spatial and temporal differences in plant part production are likely to exist between logged and unlogged forest, and may have important consequences for blue monkey food availability. Secondly, and as a direct result of these food availability differences, it is expected that dietary composition and activity patterns will differ between blue monkeys in logged and unlogged forest. Foraging strategies, manifest in total range size, activity patterns and patterns of range use are also predicted to be influenced by diet and food availability. The main hypothesis states that the long term effects of logging will result in an increase in population density of blue monkeys in Budongo by increasing the food availability and habitat suitability. The effects of logging on wildlife populations and habitat carrying capacity will then be discussed and an attempt made to describe the pattern of the post logging population density increase. In this discussion, it is stated that the particular circumstances leading to this effect are specific to Budongo and may not apply elsewhere. However, some general principles may be relevant to integrated conservation and timber harvesting in Uganda's remaining forests.

Finally, in the context of forest regeneration following logging I will test the hypothesis that blue monkeys are more likely to be seed destroyers rather than seed dispersal agents in Budongo. This will give some indication of their relative importance in encouraging forest regeneration.

Plate 1 The Budongo Forest Reserve: looking North from Busingiro hill.

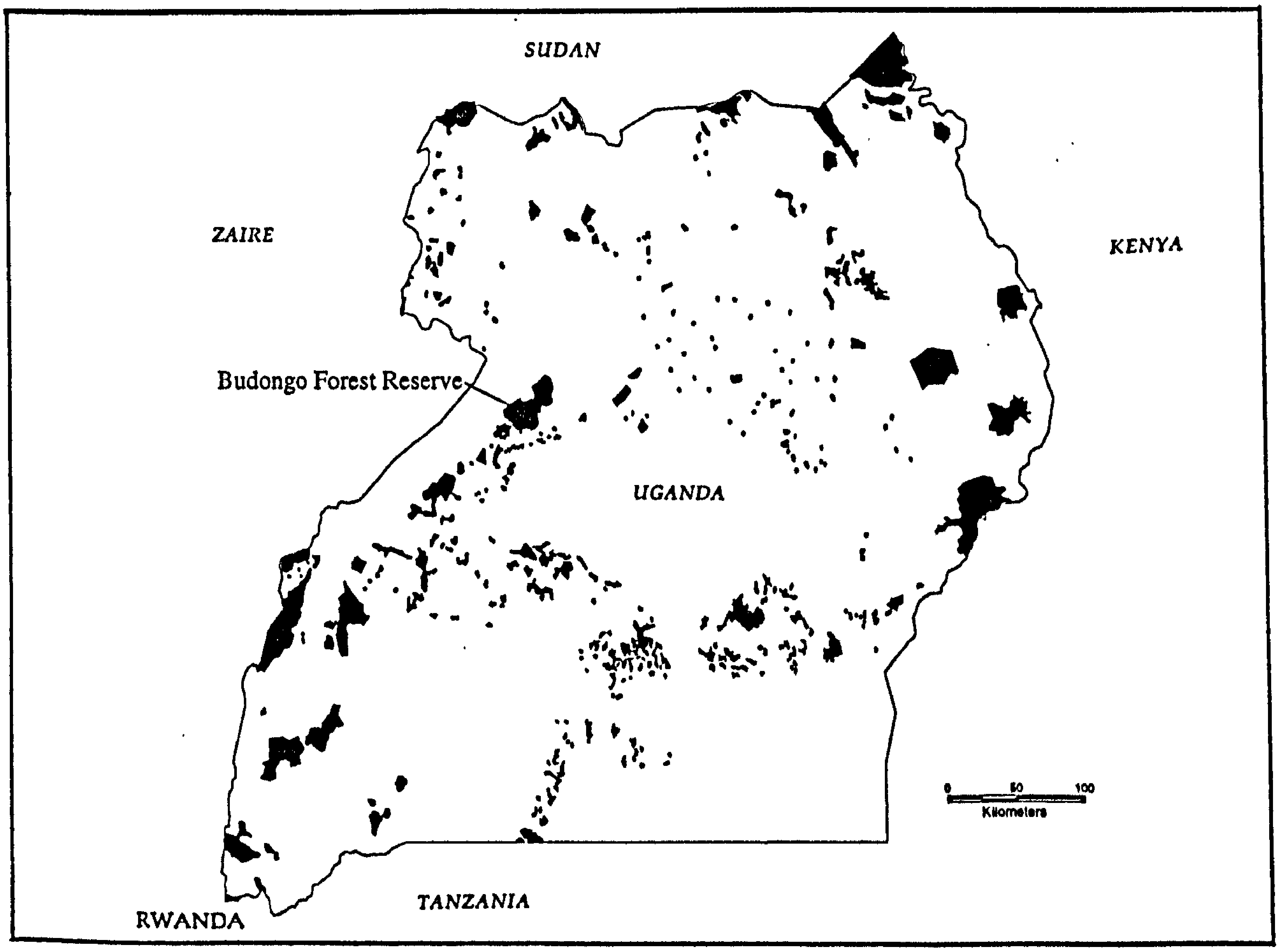
CHAPTER 2

STUDY SITE AND STUDY SPECIES

2.1 STUDY SITE

Location, Soils and Climate.

The Budongo Forest Reserve (Plate 1) lies between 1° 35'-1° 55' N and 31°18'- 31°42'E in the Masindi district of Western Uganda (Map 1). With a total area of 793km^2 (428km^2 of which is continuous forest cover) the reserve constitutes the largest and one of the most valuable timber forests in Uganda (Howard 1991). Lying on the edge of the Albertine rift valley, the forest is similar in floristic composition to the forests of the Zaire basin but also contains representatives of East African forest and savannah vegetation communities (Langdale-Brown et al. 1964).



Map 1: Location of Budongo Forest Reserve within Uganda.

Most of the forest lies between 750-1250m above sea level and occupies gently undulating terrain with a gentle slope NNW towards the edge of the Albertine escarpment. The climate of the area is tropical, with a mean annual rainfall of around 1600mm and two wet seasons, March-May and September-November. A long dry season occurs during December-February (Figure 2.1) and a shorter dry season also occurs between May-September. Annual average minimum and maximum temperatures as recorded at the Budongo Forest Project Field station range between 17-20^0 C and 28-29^0 C respectively and mean monthly temperatures are fairly constant throughout the year (Figure 2.1). Dry periods and per-humid periods [following the classification of White (1983)] are shown in Figure 2.1.

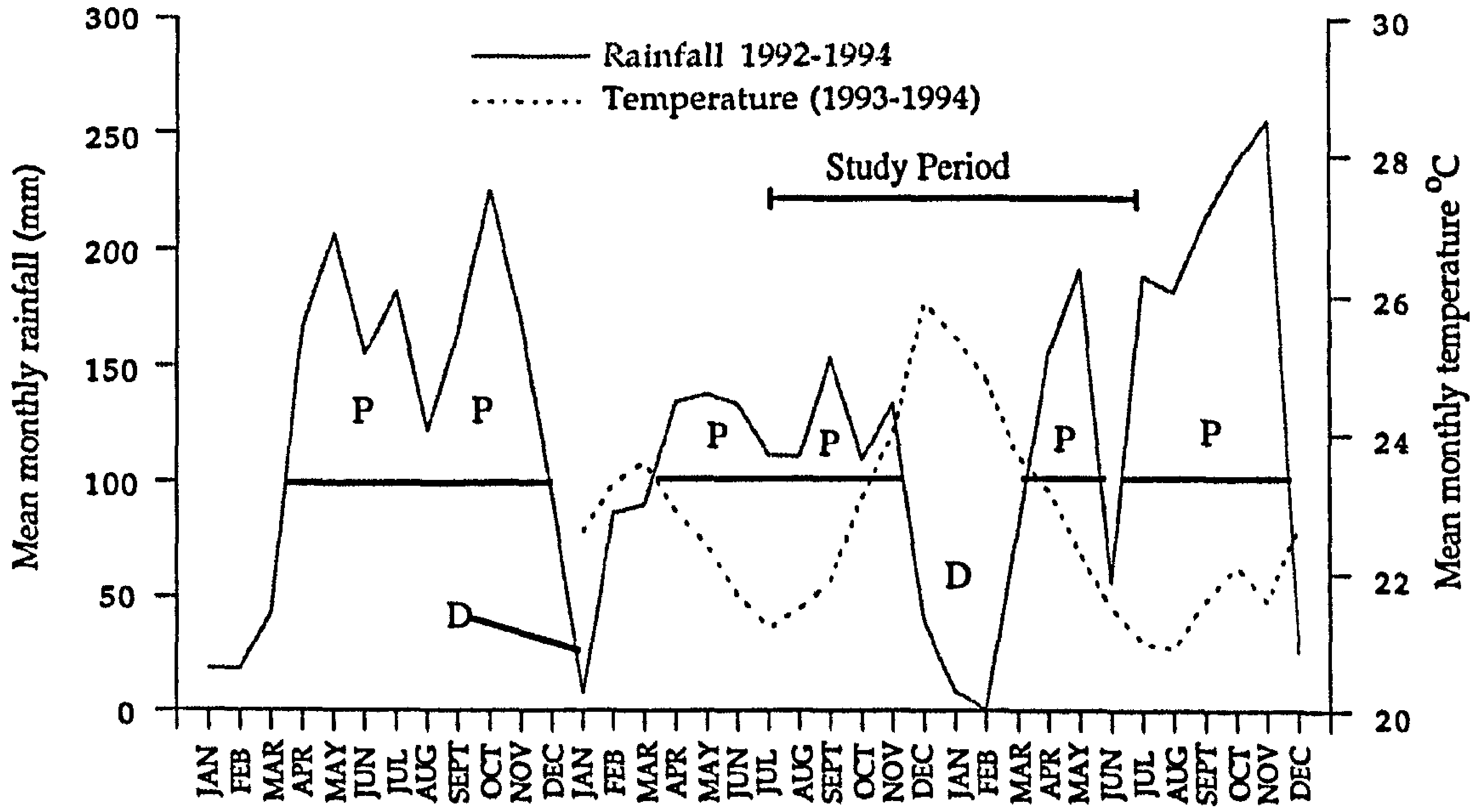


Figure 2.1. Mean monthly Rainfall (mm), 1992-1994 and Temperature (° C), 1993 to 1994 recorded at Budongo Forest Project Field station: D=dry period (when water is scarce for plants), P=Per-humid period (rainfall above 100 mm per month): after White (1983).

The climate during the 12 month study period (July 1993 to June 1994) was fairly typical of the annual climate for Budongo except for a slightly lower rainfall during one rainy season (Sep-Nov) and perhaps a drier than normal long dry season from January-March (Figure 2.2).

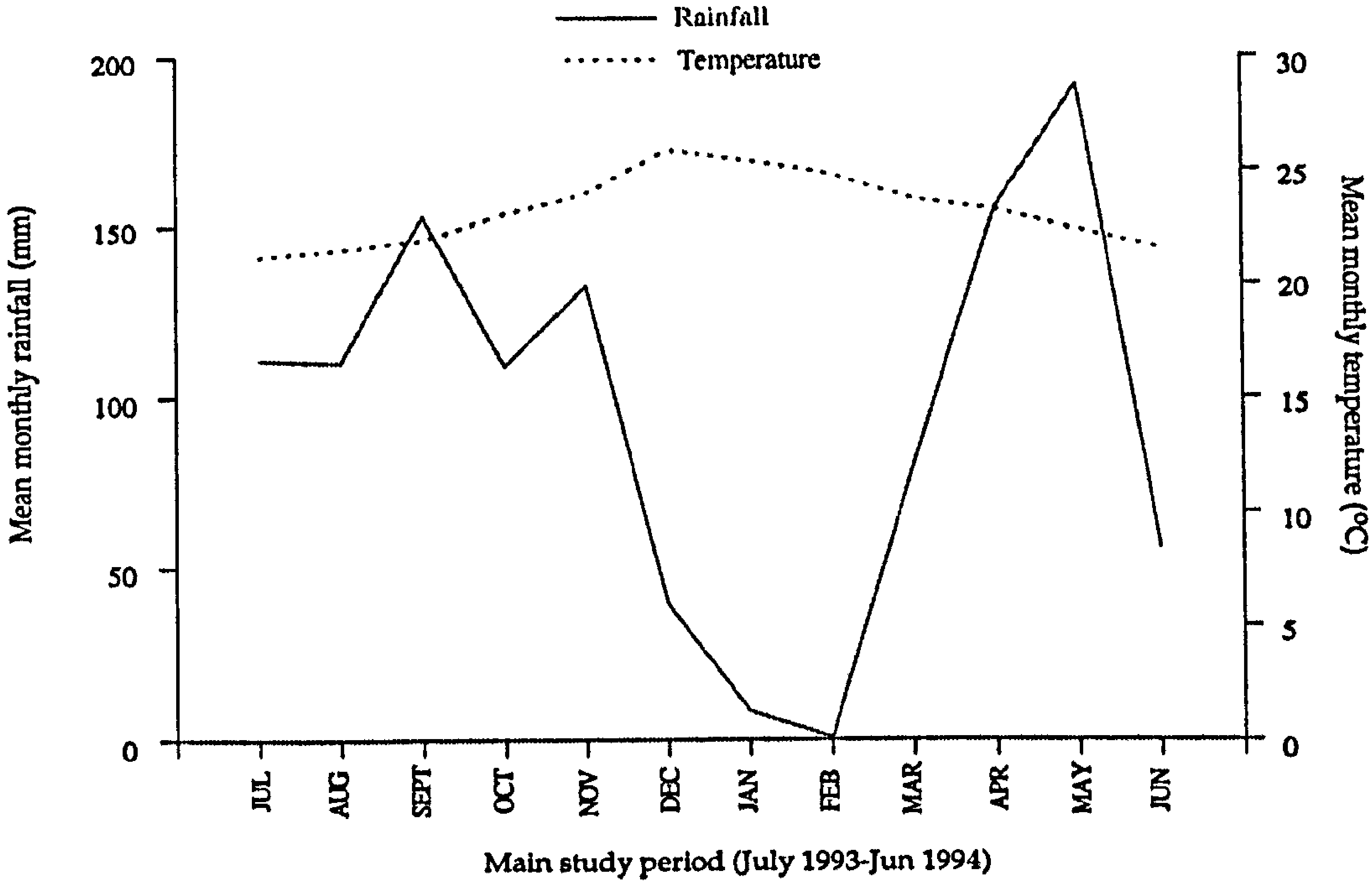


Figure 2. 2. Mean monthly Rainfall (mm) and Temperature (° C) during the 12 month study period (July 1993-June 1994).

The forest is drained by two small rivers, the Sonso and the Waisoke, both of which flow into Lake Albert and although some areas of seasonally swampy forest exist, the forest is generally dry. Underlying rock throughout most of the forest consists of gneiss's, schist's and granulites of the Basement Complex, overlain by Bunyoro Series sediments. Soils can be broadly classified into two types: ferralitic mainly sandy soils and sandy clay loams (Howard 1991).

History

There is general agreement that forest expansion across Uganda occurred around 12,000-10,000 years BP..(Hamilton 1981) following a long period of reduced forest cover due to the much drier conditions which had prevailed. During this forest expansion, which took place in a West-East direction, the forests on the

Eastern edge of the Western rift (e.g. Budongo, Bugoma, Itwara, Kibale) probably reached their maximum extent at around 8000 to 3000 years ago (Hamilton 1981, Synott 1985). Fluctuations in forest cover subsequently occurred, but the overall trend was towards a reduction in cover . The earliest records of forest clearance by man in Uganda are around 5,000 years BP. (Hamilton 1986) and deforestation has continued up to the present (Tabor et al. 1990). Archaeological work dating Bahima earthworks from neighbouring Bugoma Forest Reserve suggests that forest cover was greatly reduced during a drier period around 600 years ago (Lanning 1953). In more recent times (perhaps as recently as the last 70 years) the forests may have undergone local expansion although the exact trend is uncertain (Hamilton 1981). Dry season burning of grasslands was thought to be causing an expansion of grassland areas at the expense of forest cover and seasonal migrations of elephants from neighbouring Murchison Falls National Park may have influenced gap formation in the past (Johnstone 1969). Work currently being carried out by D.Shiel investigating forest dynamics in Budongo may shed some light on the present changes occurring and the effects of management on large scale vegetation structure (Shiel unpubl report).

Budongo Forest Reserve has a long history of management and exploitation. The Forest Reserve was officially gazetted between 1932-1939 and timber harvesting has taken place in at least 77% of the forest (Howard 1991, Synott 1985). The first commercial exploitation began as early as 1905 when visiting scientific officers noted the presence of wild rubber - *Funtumia elastica*.. Rubber was then harvested for several years until 1910 when it became commercially non-viable (Phillip and Beaton 1965). Subsequently Budongo's value as a timber producing forest was realised and selective timber harvesting using manual (pit-sawing) techniques began as early as 1915. Mechanical selective timber harvesting continued subsequently and the first major sawmill was established in 1925. Most of the timber which has been harvested from Budongo consists of mahogany (Genera: *Khaya* (one species) and *Entandrophragma* (three species)) but other species have also been extracted (Eggeling 1947b). Timber extraction and forest management continued throughout the 1940s to 1960s when Budongo represented up to 28% of Uganda's standing timber resources and supplied five sawmills (Phillip and Beaton 1965). Initially, a polycyclic selective felling system was used, but latterly this was adapted to a monocyclic system with 60 year rotation (stems >70 cm dbh being harvested). As well as harvesting mahogany, the Forest Department also carried out extensive mahogany replanting and silvicultural treatment in regenerating forest (e.g. cutting climbers, poisoning unwanted tree species). One of the key principles of the management applied in Budongo was to break up the Mature forest type and encourage a return to Colonising and Mixed Forest which supported a higher density of mahoganies (Phillip and Beaton 1965).

Timber harvesting continued throughout the 1970s and 1980s, but the effectiveness of the Forest Department was considerably eroded due to a general decline in law and order in the country together with greatly reduced funding (Hamilton 1984, Howard 1991). Sawmills found it increasingly difficult to operate under such conditions and timber processing was greatly reduced as a result. In addition, levels of illegal timber felling increased during this period. Attempts have been made in the late 1980s and 1990s to restore the ability of the Forest Department to manage its forests, and in recent years, the management of Budongo has once more become a priority (Howard 1991). In addition to re-marking boundaries, carrying out research and monitoring timber extraction by sawmills, an ecotourism program has been initiated. Despite these positive steps there still remains a widespread problem of illegal timber extraction by pit-sawyers.

Despite the fact that such a large proportion of Budongo has undergone some form of selective felling and/or silvicultural treatment, part of the management also included the setting aside of strict Nature Reserves where timber harvesting or other forms of exploitation are controlled. Research plots were also established between 1933-1944 to study growth and forest dynamics (Phillip and Beaton 1965) and some of these are important in monitoring forest dynamics (Shiel unpubl. report).

Vegetation

Due to its position in a transitional zone between the forests of the Zaire basin and the savannahs and woodlands of drier East Africa, Budongo is one of the most botanically diverse Forest Reserves in Uganda. Synott (1985) listed a total of 240 tree species, 246 terrestrial herb species and numerous epiphytes, lianas and shrubs. Howard (1991) stated that Budongo is probably the most important forest in Uganda for tree species conservation. There also exists an extensive series of floras for the forest arguably making it one of the best studied forests in Africa from a botanical point of view (Synott 1985).

The forest can be broadly classified as medium altitude semi-deciduous (Langdale-Brown 1964) and consists of several distinct vegetation communities

Plate 2. A view of unlogged forest, Compartment N15, showing sparse undergrowth and heavy shading *Cynometra* canopy.

Plate 3. A view of logged forest, Compartment N3, showing dense undergrowth and heterogeneous forest structure.

(see Eggeling 1947a, Langdale-Brown 1964 for details). These communities represent three main stages of succession: colonising forest, mixed forest and *Cynometra* forest (succession taking place in that order). Following logging, a fourth vegetation community, mixed-exploited forest, can also be recognised. In addition, areas of swamp forest and wooded grassland exist locally throughout the forest reserve where conditions are suitable. The original classification of these vegetation types has remained little changed since they were first published by Eggeling (1947a) and they are described in detail elsewhere (Langdale-Brown 1964, Synott 1985).For the purpose of this study a brief description of the main vegetation types in the two study sites follows:

Mixed-Exploited forest (Plate 3): This forest type occurs throughout Budongo following logging but is broadly similar to mixed forest which may have existed with naturally occurring disturbances (eg wind throw or lightning strikes). As in Mixed forest stands, common species are *Alstonia boonei* , *Celtis* spp., *Chrysophllyum albidum* , *Funtumia elastica* , *Ficus* spp., *Trichilia* spp.. This forest type has a high tree species diversity together with a much more diverse and heavy undergrowth. Mahoganies are abundant in Mixed forest, but being the main species removed during timber felling, they are less abundant in Mixed-exploited forest.

***Cynometra*-Mixed forest (Plate 2)**: Thought to make up about 30 % of total forest cover when Eggeling classified vegetation types in Budongo(1940's), but since reduced in extent this forest type is thought to be the climax vegetation type in Budongo. Classified as a mono-dominant forest (Connell and Lowman 1989, Hart et al. 1989) with *Cynometra alexandri* as the dominant species, other species such as *Lasciodiscus mildbraedii* , *Rinorea ilicifolia* are common in the understorey. Other common species include *Celtis mildbraedii* , *Celtis zenkerii* and *Strychnos mitis*. The understorey and ground vegetation is much more open with fewer species of herb and shrubs probably due to the heavy shading of the *Cynometra* canopy.

A comparison of aerial photographs from the 1950's and 1990 has shown that the extent of *Cynometra* and *Cynometra*-mixed forest was greater prior to much of the logging and subsequent arboricide application which has been carried out. This reduction in the amount of these forest types has corresponded with an increase in the amount of Mixed and Mixed Exploited forest (Plumptre et al.1994).

Fauna

In common with other Ugandan Forest Reserves, the fauna of Budongo does not show the same species diversity as forests further west through the Zaire basin or those in West Africa, but is important in an East African context (Hamilton 1988). Howard (1991) reports 159 species of bird, (some of which are restricted to Budongo and the few other forests in the west of Uganda) and 42 species of swallowtail butterfly occurring within the reserve. The chimpanzee population may be the largest single one in Uganda and the forest is also noted for the presence of other rare or threatened species: eg. Nahans francolin, African giant swallowtail butterfly and leopard (Howard 1991).

Mammal lists are relatively well known (see Howard 1991 for details) and are fairly similar to other Ugandan forests. Kingdon (pers. comm.) observes that Budongo, being a relatively young, low diversity forest, probably has a fauna largely derived from colonising forest species. The primate fauna of Budongo consists of 5 species - the Redtail monkey (*Cercopithecus ascanius schmidtii* Matschie), Blue monkey (*C.mitis stuhlmannii* Matschie), Black and White colobus (*Colobus guereza occidentalis* Rochebrune), Baboon (*Papio cynocephalus anubis* Fischer), and Chimpanzee (*Pan troglodytes schweinfurthii* Blumenbach). Vervet monkeys (*Cercopithecus aethiops* Gruppe) also occur around the forest edge but are not frequently observed within the forest. Although illegal hunting still continues within parts of the forest and 'accidental' chimpanzee snare wounds are quite common, primates are generally not hunted for meat in Budongo. Previous short-term studies of primate species have been carried out in Budongo (Albrecht 1976, Aldrich-Blake 1970, Marler 1969, Reynolds and Reynolds 1965, Suzuki 1979) although most of these studies were qualitative and concerned with collecting auto-ecological information. Therefore until the Budongo forest project began there had been little or no research carried out examining the effects of logging on the fauna.

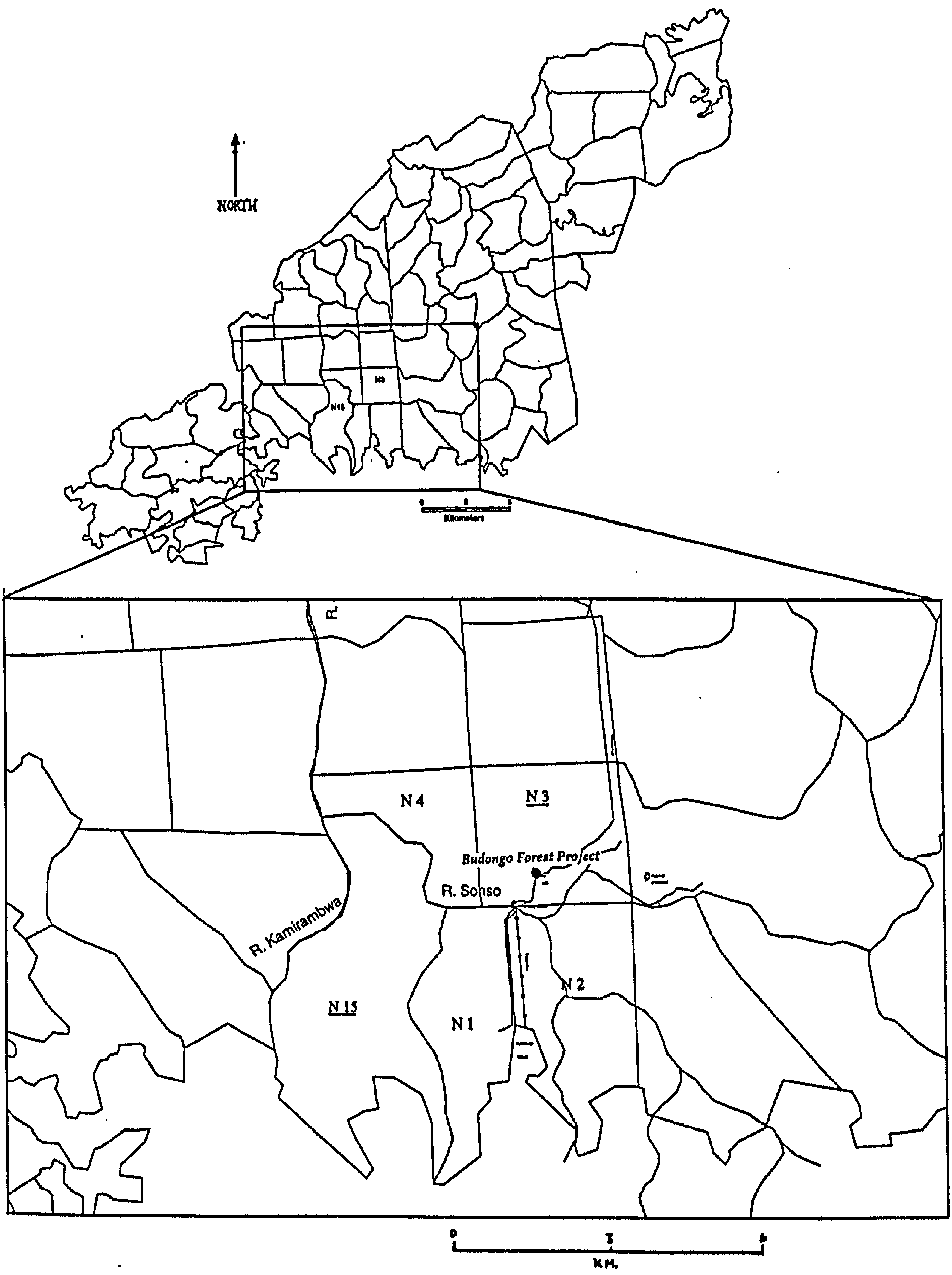
The Budongo Forest Project

During the years from the 1940s to 1960s, a large amount of research classifying vegetation and investigating vegetation ecology in relation to timber production was carried out in Budongo (Eggeling 1947b, Treneman 1954, Johnstone 1969). There was however little active research into the effects of logging disturbance and subsequent vegetation change on wildlife communities. The Budongo Forest Project was initiated in 1991 to address this lack of prior research (Reynolds 1992). The main aim of the project was to investigate the responses of wildlife to habitat modification following logging and the role of fruit eating primates in forest regeneration (see Plumptre et al. (1994) for details). Initial research focused on chimpanzee ecology in logged and unlogged forest (Bakuneeta unpubl.) and primate densities in logged and unlogged forest (Plumptre and Reynolds 1994). Research has subsequently diversified into examining the effects of logging on other groups (squirrels, birds, bats), and habitat preferences of primates (A.Plumptre pers.comm.).

2.2 LOCATION FOR THIS STUDY

In order to compare the ecology of blue monkeys in logged and unlogged forest, two adjacent study sites were chosen (Map 2). Both study sites have the same gently undulating topography and lie at approximately the same altitude. Rainfall is likely to be very similar and although there are some differences in soil conditions, there is no clear relationship between soil differences and vegetation differences (Walaga 1993). Examination of aerial photographs of the logged compartment [N3] taken prior to logging (1940's), show that it was predominantly *Cynometra*-Mixed forest and therefore was probably floristically similar to the unlogged compartment [N15] (Plumptre et al 1994).

Prior to this study, a grid system of approximately 100 x 100m trails had been cut in compartment N3 and existing trails in compartment N15 were extended to form a similar grid system. These trail systems were mapped and 1:3000 scale maps drawn. Both sites probably experience low levels of snaring for bush meat, but it is almost unknown for primates to be hunted for bush meat as there is a widespread taboo against eating primates amongst the majority of ethnic groups living around the Forest Reserve (C.Hill pers. comm.).



Map 2 : The Budongo Forest Reserve showing Compartments N3 and N15.

SITE 1: The logged site (Compartment N3: Map 2) consists mainly of Mixed-exploited forest (Plate 2) and has a total area of 585 hectares. It was selectively felled in 1947-1952 and felling in this compartment was carried out at one of the heaviest intensities across the whole of Budongo, 80m^3 of timber being removed per hectare† (Eggeling 1947b). Approximately half of the timber felled was 'Mahogany': *Khaya anthotheca, Entandrophragma angolense, E.utile* and *E.cylindricum,* while other species felled for timber included : *Alstonia boonei, Cynometra alexandri, Albizia coriara, Milicia excelsa, Cordia milleni, Erythrophleum guineense, Lovoa brownii, Morus lactea, Riciniodendron heudelotti, Maesopsis eminii, Mildbraedeodendron excelsum,* (Treneman 1954). Subsequent to felling, silvicultural operations in 1959-1961 involved application of both 'liberation' and 'refining' treatment. Liberation involved the poisoning* of 'undesirable' species in the vicinity of 'desirable' species which were of 6 feet or more in height or had a girth of 5" or more (Phillip and Beaton 1965). This was aimed at enhancing the growth of selected individuals of desirable timber species. Refining involved poisoning* of all undesirable species with a girth over 3". This was therefore a less selective procedure and was designed to remove all individuals of weed species over a certain size. Replanting of mahogany seedlings was also carried out in compartment N3 in an effort to increase the density of mahogany stems.

† This equates to approximately 3 large mahogany stems per hectare.

* Poisoning (both treatments) involved the use of arboricide/diesel mix applied with a hand sprayer.

SITE 2: The unlogged site (Nature Reserve N15: Map 2) consists mainly of Cynometra-Mixed forest (Plate 3) and has a total area of 750ha. This compartment is situated approximately 4.5 kilometres to the West of N3 (see Maps 2) and was gazetted a Nature Reserve in 1930, when Budongo was first declared a Forest Reserve. There has been no mechanised felling of timber within the Nature Reserve. Some illegal pit-sawing may have taken place in the past, but at present there are few signs of any such activity. This forest therefore represents the undisturbed natural climax vegetation type in Budongo (Eggeling 1947a).

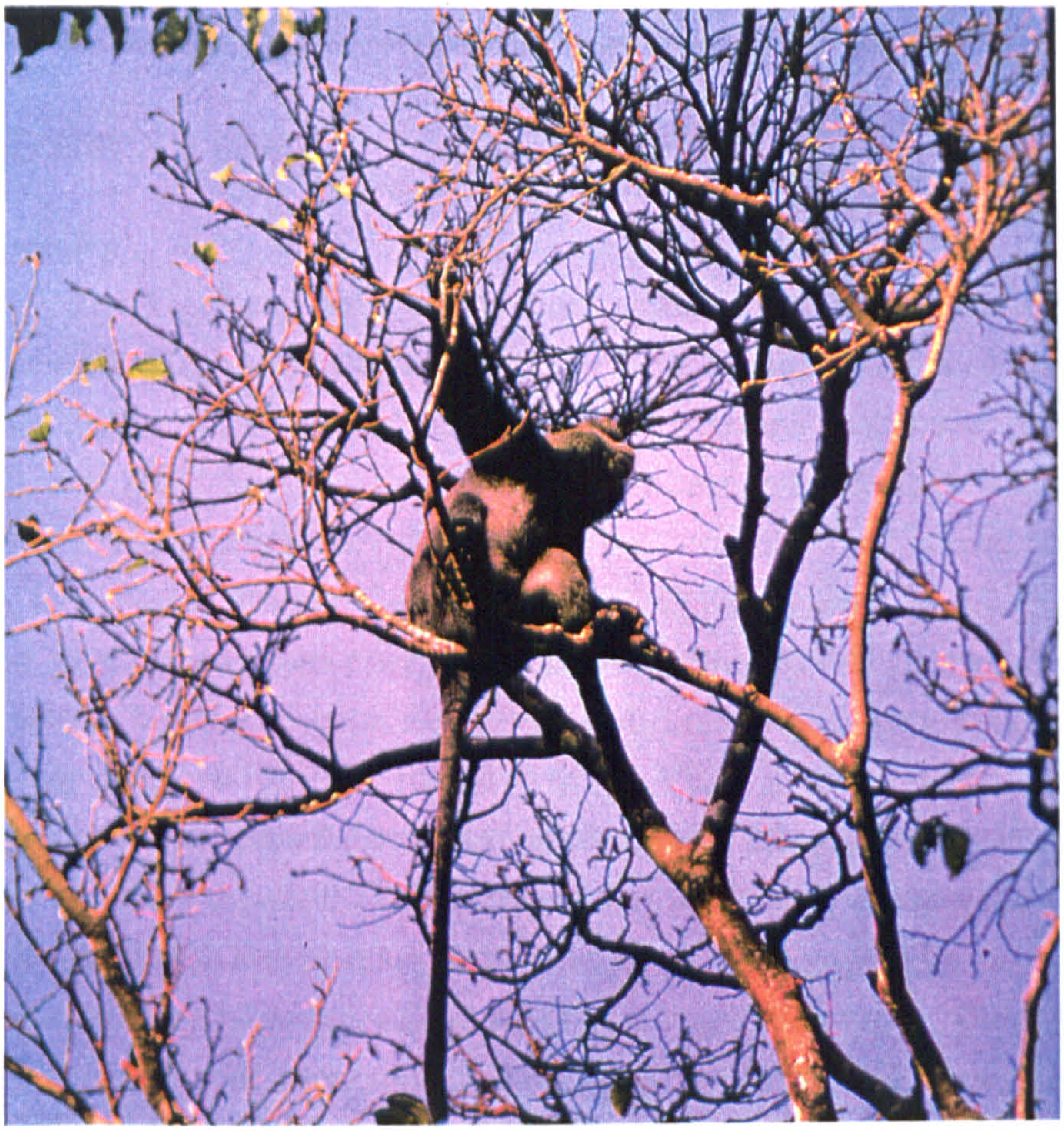


Plate 4.a. Adult male blue monkey (*Cercopithecus mitis stuhlmanni*), Group N32.

Plate 4.b. Adult female blue monkey (*Cercopithecus mitis stuhlmanni*), Group N32.

2.3 THE STUDY SPECIES

Taxonomy

The Ugandan race of the blue monkey (Plate 4. - *Cercopithecus mitis stuhlmanni* ; hereafter referred to as the 'blue monkey') is a member of one of the most diverse super species of the African guenons (Lernould 1988, Sineo 1990, Wolfheim 1983). There is some theoretical debate as to whether this super species is further divided into three species groups: C.*nictitans* , C.*mitis* and C.*albogularis* ; or only two species groups: C.*nictitans* and C.*mitis/albogularis* (see (Lernould 1988 and Sineo 1990 for taxonomic reviews). Recently, Sineo (1990) presented evidence for a distinction between C.*mitis*, C.*nictitans* and C.*albogularis* karyotypes but suggests a super specific grouping for the three forms. The C.*mitis* super species (sensu Sineo 1990) has a wide distribution through Southern Ethiopia, Central and East Africa as far south as Malawi and Southern Africa [C.*mitis erythrarchus* or samango] (Wolfheim 1983). Sub species of the C.*mitis* group occupy a broad range of habitat encompassing a large altitudinal range and vegetation types. These range through coastal dune forest, montane bamboo forest, and lowland forests with a range of altitudes and rainfall (see Table 2.1).

Ecology

The evolution of all African guenons is thought to be a very recent phenomenon and there is a growing body of evidence that suggests that the C.*mitis* group is one of the most recently divergent amongst the Cercopithecini (Leakey 1988, Lawes 1990, Sineo 1990). It is also probably one of the more recent species to occupy a forest niche. Blue monkeys in Uganda are therefore likely to be very recent colonisers of forest habitat. At present the blue monkey occurs in eleven of Uganda's major Forest Reserves as well as many of the smaller forest reserves (Howard 1991) in a range of forest types, with two different sub species (C.*mitis kandtii* and C.*mitis doggetti*) occurring in higher altitude forest in the South west of the country (Aveling 1984, Butynski and Kalina 1993).

There have been several detailed studies carried out on the general ecology of the C.*mitis* group and there is considerable information on group structure, diet, activity and ranging patterns (Butynski 1990, Cords 1986a, 1987, 1988, Lawes 1990, 1992, Rudran 1978). Where previously studied, C.*mitis* shows some variation in population density, group size and range size (see Table 2.1).

Table 2.1. Comparative estimates of population density, group size and other ecological parameters from previous studies of *C.mitis*.

Study site (Author)	Group size (mating system)	Range size (ha)	Density (no./km^2)	% Fruit in diet	Forest type
Budongo, Uganda. (Aldrich-Blake, 1971)	13.3 * (five one male, one two male)	8.04 *	---	----	Medium altitude moist semi-deciduous
Budongo, Uganda (Plumptre et al. 1994, this study)	11.25 *	12.81 *	43.9 (mean for Budongo)	50.35 *	" "
Kibale, Uganda. (Struhsaker 1978)	25 (one male)	60.5 - 73	41.75	42.7	Medium altitude moist evergreen/ semi deciduous
Kibale, Uganda. (Rudran 1978a)	20.8 * (three one male, one two male)	72.05 *	----	42.7	" "
Kibale, Uganda. [1] (Butynski 1990)	Kanyawara 18.25 *	33.0 *	53.36	27.7	" "
	Ngogo 15 * (all one male)	253 *	4.5	30.1	
Kakamega, Kenya. (Cords 1987)	45 (one male)	37.75	169	65.6	Drier type lowland rainforest.
Diani, Kenya. (Moreno-Black and Maples, 1977)	18-22 (one male)	----	----	57.1	Coastal lowland dry forest
Muguga, Kenya (DeVos and Omar 1971)	16.3 * (one male)	13.7 *	118.9	----	Dry upland evergreen forest
Kahuzi, Zaire. (Schlichte, 1978)	12.33 * (one male)	25 *	----	37	High altitude mountain forest
Ituri, Zaire. (Thomas 1991)	4-16 n/a	----	24.2 ± 7.5	----	Lowland rainforest
Zomba, Malawi. (Beeson 1985)	11 19 (one male)	8 25	16-40	42.1	Evergreen montane forest
Cape Vidal, S.Africa. (Lawes 1991)	30-35 (one male)	15	202	51.7	Indian Ocean coastal belt dune forest.
Ngoye, S. Africa. (Lawes et al. 1990)	16 (one male)	----	48	91.1	Coastal scarp forest

NOTES
* = Mean for several groups.
1. Two study sites, one with a high density population, one with a low density population.

As shown in Table 2.1 the density estimate for Budongo lies in the mid-range of densities estimated at various other sites. This estimate for the whole forest is calculated across several different compartments (Range=7.7 ind/km^2 to 85.9 ind/km^2 (Plumptre et al. 1994)).

Group structure in *C.mitis* is broadly based on matrilineal female groups with normally one resident male (Cords 1988). However, there is growing evidence that the mating system may not be as rigidly one male as previously thought (Rowell 1988). Seasonal influxes of extra-group males has been reported in two sites by Henzi and Lawes (1987) and Cords et al. (1986). Group size has been shown to vary considerably and it is likely that the quantity and distribution of food resources determines the number of females in the group (sensu Wrangham 1980). Diet and activity patterns also vary depending on habitat quality, seasonality of climate and other factors (Beeson 1989, Cords 1986, Lawes 1992, Lawes and Piper 1992). Lawes (1992) reported that activity budgets in samangos (*Cercopithecus mitis erythrarchus*) were determined largely by food abundance, temperature and daylength, concluding that a great deal of flexibility exists within the species. Generally speaking, the major component of the omnivorous diet consists of ripe and unripe fruit, supplemented by young leaves, buds, insects and flowers. Periods of dietary stress have resulted in the exploitation of unusual food sources such as bark (Beeson 1986) and even vertebrate prey such as mice (Wahome et al 1988).

Previous accounts of seed treatment by blue monkeys classify them primarily as seed destroyers (Rowell and Mitchell 1991) although like other Cercopithecines they do make extensive use of cheek pouches to process fruit, discarding intact seeds after removing pulp. Range sizes vary considerably (Table 2.1) and in general group ranges are exclusive with some degree of overlap occurring at the extent of a group's range. Females appear to play a major role in defending these ranges (Butynski 1982b, pers. obs.), as has been suggested for other arboreal guenons (Hill 1994).

CHAPTER 3

GENERAL METHODS

3.1 DAWN TO DUSK FOLLOWS

Commencing in February 1993 four groups (two within the trail systems of each compartment) were selected, and habituation of these groups was initiated. Prior to habituation, the same groups were consistently found by searching in the vicinity of where a group was last contacted. As habituation and preliminary observations progressed, groups could be identified by i) their composition ii) individuals with recognisable features and iii) the loud calls of the male (see Butynski et al. 1992).

Once the four groups were considered to be well habituated to observers (May 1993), 12 hour follows were commenced by myself and Geresomu Muhumuza. The original aim was to follow each of two groups for five consecutive days per month. There is in fact no apparent logical reason for choosing a five day sampling regime, but it appears to have become widely accepted as the conventional method. However, since this study was extended to include four groups, it was logistically easier to carry out follows of two consecutive days per group at two week intervals (four days per month per group). Choice of four groups instead of two was aimed at providing a wider database with which to make comparisons regarding diet and ranging patterns. Basing dietary analyses on only one group may have given rise to a bias in diet due to local preferences (Chapman and Fedigan 1990) and individual group ranges may also vary considerably.

Scan Sampling

The four groups were identified by the following codes and will be referred to using these codes throughout the thesis:

N31	Group 1; logged compartment N3
N32	Group 2; logged compartment N3
N151	Group 1; unlogged compartment N15
N152	Group 2; unlogged compartment N15

Groups were located on the evening prior to carrying out a follow and then were relocated the following morning at approximately 7am. Follows continued until 7pm or until poor visibility early in the evening meant that age/sex classification was difficult. Data collection was suspended during periods of heavy rain when it became difficult to observe the group and record scan data. During such periods, the monkeys usually retreated to thick vegetation and remained fairly inactive. Groups usually settled for the night before or around 7pm and thus could be located in the same locality the following day.

During dawn to dusk follows, the group was scanned (using 10 x 40 binoculars) from left to right every 15 minutes, starting on the hour. Scans lasted 10 minutes or until five individuals had been sampled, whichever came first. This sampling technique reduces biases in over-sampling individuals or activities which are more obvious to observers. When an individual was detected during a scan, the first discernible activity lasting for more than five seconds was recorded. If the individual's activity could not be determined after one minute had elapsed, the next individual was sampled. Individuals were assigned to age-sex classes consistently by both observers based on physical characteristics. The only difficulty involved in distinguishing between age-sex classes was when infants began to spend more time independent of their mother. At this stage they may have been classified as juveniles when moving independently but later classified as infants if picked up and carried by the mother. Any observed changes in group composition were recorded when first detected and in some cases demographic changes such as death, emigration or immigration were inferred from the disappearance/appearance of individuals.

For each individual sampled, the following information was recorded:

Age-Sex Classes

ADM: Adult male,: 5 yrs and above. Larger body than adult females and immature males, well developed whitish whiskers.

ADF: Adult female: 3yrs and above. Nipples prominent, cycles noticeable, body smaller than adult male but larger than a sub adult.

SA: Sub Adult: between 1.3 and 3/5 yrs (females and males respectively).Sexes were identified where possible, males having larger body size than females and sometime identifiable by their attempted adult male vocalisations.

JUV: Juvenile: much smaller than Sub adult but moving independently of mother.

INF: Infant: Still dependant on mother, often carried and still unweaned.

Activities

Feeding: active handling or ingestion of food including chewing or processing in cheek pouches.(FE)

Foraging: searching or manipulating plant material in the apparent search for food.(FO)

Resting: body stationary, monkey sitting, standing or lying not engaged in any other activity (REST).

Moving: travelling outside a food patch: moving entire body, not foraging(MOV).

Vigilant: head up, not feeding or foraging, but watchful for predators or other groups (VIG).

Grooming: Either self grooming (SG), subject as groomer (SGR) or subject as groomee (SGE).

Playing: (PLAY).

Vocalising: Either males making loud 'pyow' calls or females involved in inter group territorial aggression (VO).

Height In Canopy

LOW:	0-10 metres
MID:	11-20 metres
HIGH:	21-30 metres.
EME:	30 metres and above, emergent trees, not part of continuous canopy.

Food Items

When an individual included in the scan was feeding, a tree species code and an item code were recorded. Tree species codes were those already used by other members of the Budongo Forest Project and item codes were as follows:

ML:	mature leaves
YL:	young leaves
LP:	leaf petiole
BU:	leaf buds
UF:	unripe fruit
RF:	ripe fruit
FL:	flowers
INV:	invertebrate food
SEED:	seeds
BA:	bark
VERT:	vertebrate food
FUNG:	fungus
LI:	lichens

After sampling five individuals or ten minutes had elapsed (see above) the following group information was recorded:

- Location of the centre of mass of the individuals sampled was marked on a map (scale 1:3000).
- Weather conditions coded as sunny (SU), overcast(OV), cloudy (CL), heavy rain (HR), light rain (LR), windy (WI), or a combination of the above codes.
- Association/Interaction with other species, coded as Black and white colobus (BWC), Redtail monkey (RT), Baboon (B) or Chimpanzee (CH).

Additional *ad libitum* records of 'rare events' such as mating, eagle attacks, infanticide etc. were made and dung samples were collected opportunistically for subsequent analyses (see Chapter 7: Seed Dispersal).

Despite random sampling being used, some age-sex classes in the four groups were not sampled as frequently as expected. Previous studies of blue monkeys (Cords 1987, Lawes 1992) have shown some differences in the dietary composition and activity budgets between age-sex classes. In order to reduce bias in the data from certain age-sex classes being over-sampled in one group compared to another, data were corrected (described in Chapter 4).

3.2 VEGETATION

In order to investigate differences in forest structure, species composition and abundance, vegetation plot enumeration was carried out in the home range of two of the study groups (one in logged forest and one in unlogged forest). Given the relatively small size of the ranges used by all four groups (see Chapter 8) it was decided to enumerate two ranges (one from each compartment) in detail by sampling all of the home range area used during the study. Vegetation sampling was not started until after 10 months of group ranging data had been collected in order that the range of the two groups was reasonably well established. In order to avoid sampling unrepresentative areas of the group range, vegetation plot analyses were confined to areas of the range where groups had been regularly recorded while areas on the periphery of the known range were excluded.

Within each range 25 x 25m plots were laid out on a grid system on North-South/East-West axes. The position of each plot was recorded on the appropriate 1:3000 scale trail grid map. A plot size of 25 x 25m was selected to give a practicable size of plot in which to measure all trees easily and, if necessary, data from several adjacent plots could be pooled to give a larger sampling unit.

Within each plot every tree over 10 cm diameter at breast height (dbh) was identified and the dbh recorded in centimetres. Buttressed trees were measured at 1.5m from the ground. As well as recording species identification and dbh, each tree was classified into a 5 metre height category from 1-7 by visual estimate:

Tree height categories (m)

1....................0-5
2....................6-10
3....................11-15
4....................16-20
5....................21-25
6....................26-30
7....................30 and above.

Individual trees were scored for presence of climbers/lianes where a score of 1 meant few climbers were present and a score of 4 meant heavy climber cover in the tree.

Botanical samples were collected from unidentified individuals and were subsequently identified either using the Budongo Forest Project herbarium (compiled by A.Plumptre) or at the Makerere University Herbarium. Some specimens remained unidentified, these are referred to below by their code number.

3.3 PHENOLOGY

To document and compare seasonal availability of mature leaves, young leaves, fruit and flowers in the two sites, selected trees were monitored every two weeks and scored for production. Trees selected for phenological observations were those known to be important as food for blue monkeys [from Aldrich-Blake's (1970) food species list and A.Plumptre unpubl. data]. Although some of these species were later found not to be used extensively, trees producing the major food items were all included (see Chapter 6). Trees were sampled in two ways: firstly, phenology trails were established where individual food trees of dbh > 30 cm were tagged 5m either side of the trail for monitoring. One trail was established in each compartment, passing through the ranges of both groups in the compartment. The N3 phenology trail was 2.45km long and the N15 phenology trail was 2.6km long.

The second sampling technique involved marking out ten 20 x 50m plots randomly located within the ranges of the four groups and tagging any tree greater than 30cm DBH used as food. This resulted in 40 plots, 20 in each site, 10 in each range. In both cases, only healthy trees with easily visible canopies were chosen to ensure accurate scoring by observers.

To ensure consistency between observers (myself and Geresomu Muhumuza) tree scoring was carried out on a representative subset of trees and scores compared subsequently. Any differences in scoring were then discussed and standardised. The scoring system used was the same as that employed by A.Plumptre, C.Bakuneeta and other researchers in the Budongo Forest Project as well as researchers in other tropical field sites (Chapman et al 1992, 1994).
Scores were on a 0-4 scale as follows for the following items:

0..................................0 % of the canopy producing the item
1..................................1-25% " "
2..................................26-50% " "
3..................................51-75% " "
4..................................76-100% " "

Trees were scored for: Mature Leaves, Young Leaves, Leaf buds, Unripe fruit, Ripe fruit and Flowers. Mature/Young leaves and Ripe/unripe fruit were distinguished on the basis of visual cues (colours, textures) as well as prior knowledge of the tree species concerned.

3.4 ANALYSES

Since the data did not satisfy the requirements for parametric statistical tests, non-parametric tests were carried out in most cases (Campbell 1989). All data were entered into files using Excel (version 4.0) for Macintosh and statistical tests were carried out using SPSS (Macintosh version). Graphs were produced on Kaleidagraph. Analyses on ranging patterns were carried out using Wildtrak (Todd 1993), a software package written for non-parametric analyses of radio tracking data on Macintosh computers.

CHAPTER 4

HABITAT COMPOSITION

4.1 INTRODUCTION

There is increasing evidence that population density, group size, and ranging patterns in primates are determined by a combination of i) the distribution and abundance of food resources and ii) predation pressure (Garber 1987, Newton 1992, Oates et al 1990, Van Schaik and Horstermann 1994, Wrangham 1980). For guenons however, predation pressure plays a lesser role in determining group size owing to the frequent formation of polyspecific associations (Van Schaik and Horstermann 1994). Formation of polyspecific associations precludes an increase in the number of males per group (hence an increase in group size) therefore predation is unlikely to be a proximate factor determining group size in blue monkeys.

On the contrary, food distribution and abundance is likely to play an important role in determining primate group size, home range area and patterns of range use (Gautier-Hion 1988, Gautier Hion et al 1981, Harrison 1983, Lawes 1992, Newton 1992, this study). The distribution and abundance of plant food resources is determined both by tree species diversity and composition within the habitat. A study of the comparative ecology of a primate species in logged and unlogged forest therefore requires an investigation of the structure and composition of the vegetation which comprises the home range of groups.

Selective logging can cause reduction in total basal area and canopy cover (Cannon et al 1994, Johns 1992) and lead to changes in the tree species composition and abundance not only for the tree species valued as timber trees but those damaged during felling operations. In addition, certain lianes and understorey species may be affected (White 1994a) and in some circumstances conditions for liane growth may be enhanced. Treefalls and branch loss rates may change following logging and influence vegetation structure and composition (Kasenene and Murphy 1991). Distribution of basal area among tree species can determine relative food availability (Chapman et al. 1994) and estimates of food availability derived from basal area estimates can be useful predictors of carrying capacity. The structure of the forest can also influence vertical ranging patterns and movement pathways of primates(Johns 1988a).

Due to the particular nature of the unlogged forest occurring in Budongo and its tendency towards mono-dominance (Eggeling 1947a, Connell and Lowman 1989), it is also of interest to discuss the direct effects of logging on this forest type. *Cynometra* forest is considered a climax vegetation type in Budongo and may become dominant in the absence of disturbance (Eggeling 1947a, Hart et al. 1989). This has important implications for the primate carrying capacity of unlogged forest and changes in carrying capacity following logging will be more easily understood if changes in vegetation can be understood. As well as being important in the context of explaining differences in primate ecology, *Cynometra* dominance and the consequences of logging can be considered in the broader context of conservation goals and objectives.

4.2 METHODS

Plot Enumeration

Vegetation plots were enumerated as described in Chapter 3 and the following analyses carried out on the data. Species-area curves for the two compartments were plotted using plots of size 0.0625 ha as sampling units for cumulative number of species. An Index of Overlap (Pielou 1966) was calculated between the vegetation in the two ranges as the sum of shared proportions of stems present. Overall species diversity was calculated using the Shannon-Weiner Index of Diversity (Pielou 1966). Total basal area and proportional basal areas were calculated for each tree species in the two ranges and species were ranked according to proportion of basal area. Using total stem number, proportions of stems in different dbh classes were calculated. As *Cynometra alexandri* appears to have a considerable effect on forest composition and original management was aimed at discouraging *Cynometra* re growth from the logged areas, frequency distribution of *Cynometra* stems in different dbh classes was plotted.

For further analyses, 0.25 ha plots were used for the calculation of i) The mean number of stems per plot, ii) The mean number of species per plot and iii) Species diversity and species evenness per plot -- using the Shannon-Weiner Index of diversity ($H = -\Sigma\, p_i \ln p_i$ where p_i is the proportion of stems for the i_{th} tree species and the Index of evenness $J = H/\ln N$ (where N is equal to the total number of species recorded in the plot).

Coefficients of Dispersion (Greig-Smith 1983) were calculated for the important food species to give an indication of the distribution of food trees and are discussed further in Chapter 7. This measure gives an indication of the departure from randomness of the particular tree species in question by calculation of a ratio of Variance:Mean. Importance values (Greig-Smith 1983) were calculated to give a comparable index incorporating measures of tree species distribution, relative density and abundance. The Importance value is the summed values of Relative density, Relative frequency and Relative dominance. These three values are calculated as follows:

a) Relative density (of individuals/stems) - gives a measure of the proportional composition by stems.

$$\text{Relative density} = \frac{\text{Individuals of species x}}{\text{Total No. of individuals}} \times 100$$

b) Relative frequency - gives a measure of the relative probability that any species will occur in any given plot (i.e.. it describes the distribution.

$$\text{Relative frequency} = \frac{\text{Frequency of species x}}{\text{sum of frequency values for all species}} \times 100$$

c) Relative dominance - gives a measure of the proportional composition by Basal Area.

$$\text{Relative dominance} = \frac{\text{Basal area of species x}}{\text{Total Basal area of all species}} \times 100$$

As the sum of these three values for the particular species, the Importance Value never exceeds 300 as each Figure is a percentage ranging from 0 to 100. Tree species were then ranked on the basis of their Importance Value and Importance Values of key food species were compared (Chapter 7).

Finally, using data collected by A. Plumptre for the whole of compartments N3 and N15 (approximately 3ha was measured in each compartment), it is possible to make a comparison of vegetation data from the group ranges with data for whole compartments (A.Plumptre unpubl.data). This comparison was carried out to assess how representative the vegetation sampled in the two ranges was of the compartment as a whole.

4.3 RESULTS

Habitat Composition

A total of 18.25 ha of vegetation was sampled in the home ranges of group N32 and N151 combined: 7.75 ha (31 x 0.25 ha plots) in the logged forest (Group N32) and 10.5 ha (42 x 0.25 ha plots) in unlogged forest (Group N151). The number of plots sampled in logged forest was fewer due to the smaller range size of group N32. Some trees remained unidentified in both samples - 0.55 and 0.261 % of stems, in N32 and N151 respectively.

A total of 141 different tree species from 31 families were recorded in both compartments. Of these 141 species, 63 occurred in both compartments, 50 were exclusive to N3 and 28 were exclusive to N15. The total number of tree species for each range was 113 and 91 for N3 (logged) and N15 (unlogged) respectively (see Appendix 1 for full list of species and families). Species overlap between the two areas, measured as the sum of shared percentages of each species (Pielou 1966) was 43.9 % and 46.4 % (using % stems and % basal area respectively). A comparison of families shows N3 has a higher number of families (31) compared to N15 (27). Families ranked by numbers of species, % of total stem number and % of total basal area are shown in Table 4.1.

Table 4.1. Summary of botanical composition of the two study sites

	N3	*N15*
No. of species	113	91
No. of families	31	27
Most common species: (% Basal area)	*Alstonia boonei,* *Celtis durandii,* *Cynometra alexandri,* *Celtis mildbraedii,* *Ficus sur.*	*Cynometra alexandri* *Celtis mildbraedii* *Lasciodiscus mildbraedii* *Celtis zenkerii* *Alstonia boonei.*
Top 5 families: (% Basal area)	ULMACEAE APOCYNACEAE MORACEAE LEGUMINOSEAE MELIACEAE	LEGUMINOSEAE ULMACEAE MELIACEAE RHAMNACEAE APOCYNACEAE
(% Stems >10cm dbh)	ULMACEAE APOCYNACEAE MELIACEAE MORACEAE EUPHORBIACEAE	LEGUMINOSEAE ULMACEAE RHAMNACEAE VIOLACEAE APOCYNACEAE
(No. species)	MORACEAE EUPHORBIACEAE MELIACEAE ULMACEAE SAPINDACEAE	EUPHORBIACEAE LEGUMINOSEAE MELIACEAE APOCYNACEAE SAPINDACEAE

The most common families in N3 by proportion of basal area and stem number are Ulmaceae and Apocynaceae. The family Moraceae contains the largest proportion of all species (followed by Euphorbiaceae) due to the presence of a high number of *Ficus* spp. as well as species such as *Morus lactea* , *Trilepsium madagascarensis* and *Myrianthus arboreus* in N3. The most common families in N15 by proportion of basal area and stem number are Leguminoseae and Ulmaceae. The family Euphorbiaceae (followed by Leguminoseae) contains the highest proportion of all species in N15 (Table 4.1) and includes species such as *Alchornea laxiflora, Croton macrostachyus* and *Riciniodendron heudelotti.*

The shape of the species area curves for the two ranges show a difference in total number of species recorded and rate of accumulation of new species (Figure

4.1). Even although fewer plots were sampled in the logged forest, after the same sampling effort (eg.7.5 ha) N3 shows a higher number of species and new species accumulation is still continuing (Figure 4.1). In N15, a lower number of species were recorded and the accumulation rate decreases after the same number of plots have been sampled.

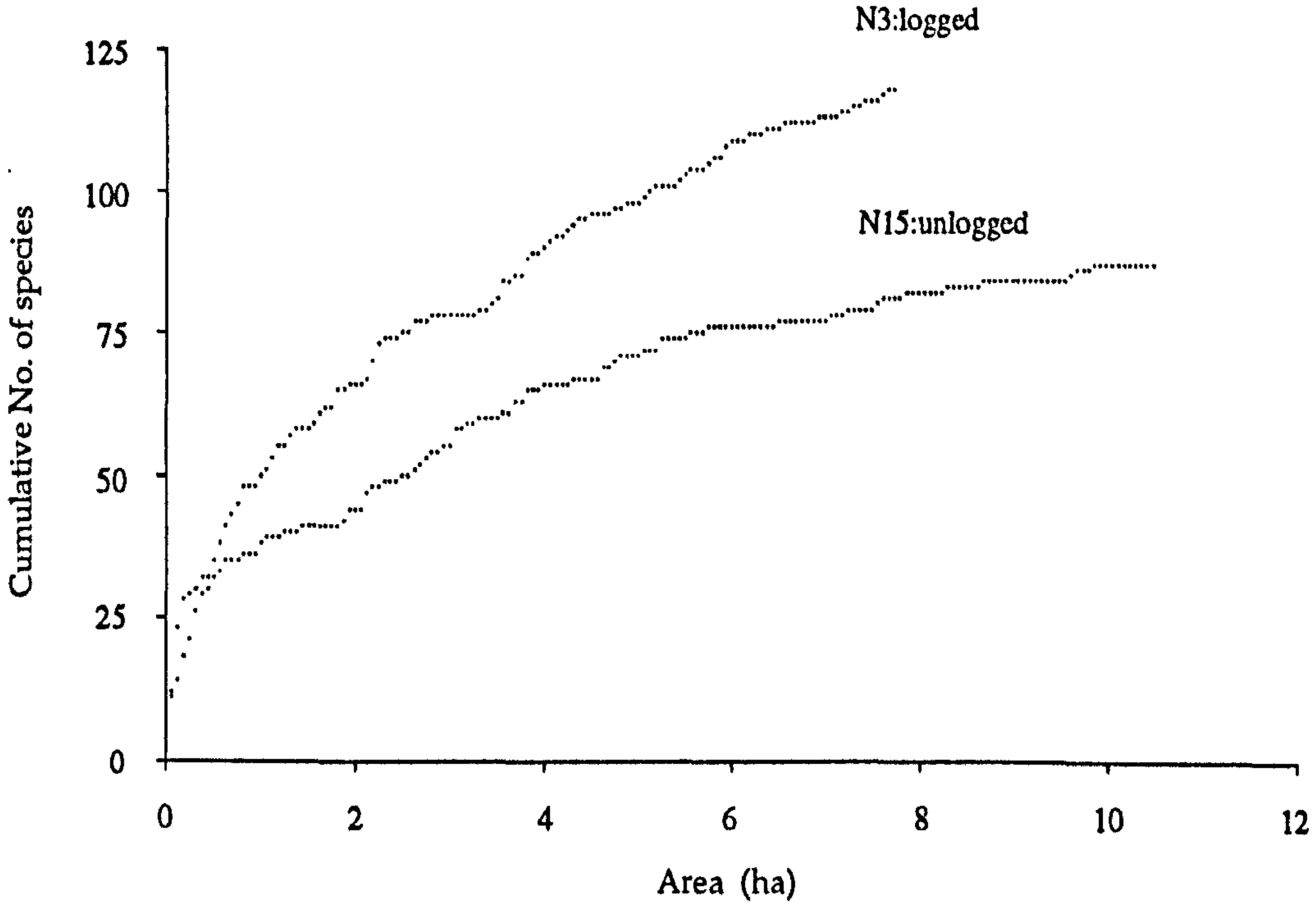


Figure 4.1. Species area curves for logged and unlogged vegetation plots within group N32 (logged forest) and N151 (unlogged forest) ranges.

Species Composition and Abundance

Comparison of summary statistics from N3 and N15 vegetation plots (Table 4.2) shows a significant difference in the mean number of species (z-test: z=11.63, P<0.01) but a non-significant difference in the mean number of stems (z-test: z=1.22, P>0.05). There was no difference in the mean basal area per vegetation plot (z=0.87, P>0.05) although N3 showed a reduction in basal area equivalent to 6.96 %. Expressed as a percentage of unlogged forest, the changes observed in logged forest can be summarised as a 6.96% reduction in total basal area, but a 4.95% increase in the number of stems per plot and a 65.12 % increase in the number of species per plot.

Shannon Weiner Indices of Diversity and Index of Evenness are also significantly higher in logged plots than in unlogged plots (Mann Whitney U=3, P<0.05; U=8, P<0.05 for diversity and evenness respectively). N3 has a higher within-plot diversity and shows more evenness within-plot (Table 4.2).

Climber scores per plot (sum of individual tree scores for the plot) were significantly higher in logged forest (Mann Whitney U=175, P<0.01). Comparison of the frequency of treefalls/branchfalls (due to wind throw or senescence) showed a slightly higher frequency in the logged compartment (8.87 % of all plots) compared with the unlogged compartment (5.36% of all plots).

Table 4.2. Summary statistics for vegetation plots (0.25 ha) in logged and unlogged forest [*]

Forest Type	*Mean no of sp.*	*Mean stem no.*	*Median Diversity index (Evenness)*		*Mean Basal area(Cm^2)*
Logged Forest	31.06[†]	147.64	2.82	(0.83)	111999 (39527)
(N32 Home range)	*19-40*	*105-218*			*47704-240816*
	(3.95)	(25.67)			
Unlogged Forest	18.81[†]	140.67	2.00	(0.67)	120385 (41496)
(N151 Home range)	*11-27*	*97-196*			*48188-285675*
	(4.781)	(21.58)			
Tests for differences	z-test	z-test	--Mann-Whitney U test--		z test
	P<0.01	ns	P<0.05	(P<0.05)	ns

[*] Range in italics, standard deviation given in brackets.

[†] Using the species-area curve gives the following estimates of species per hectare : N3=50 species/ha, N15= 38 species/ha

Basal areas for each species were calculated and expressed as a proportion of total basal area. Plotting the top ten species by proportion shows the dominance of *Cynometra alexandri* and the skewed nature of the distribution of basal area within the top ten species in unlogged forest (Figure 4.2b). By contrast, proportion of total basal area is much more evenly distributed amongst the top ten species in the logged forest (Figure 4.2a).

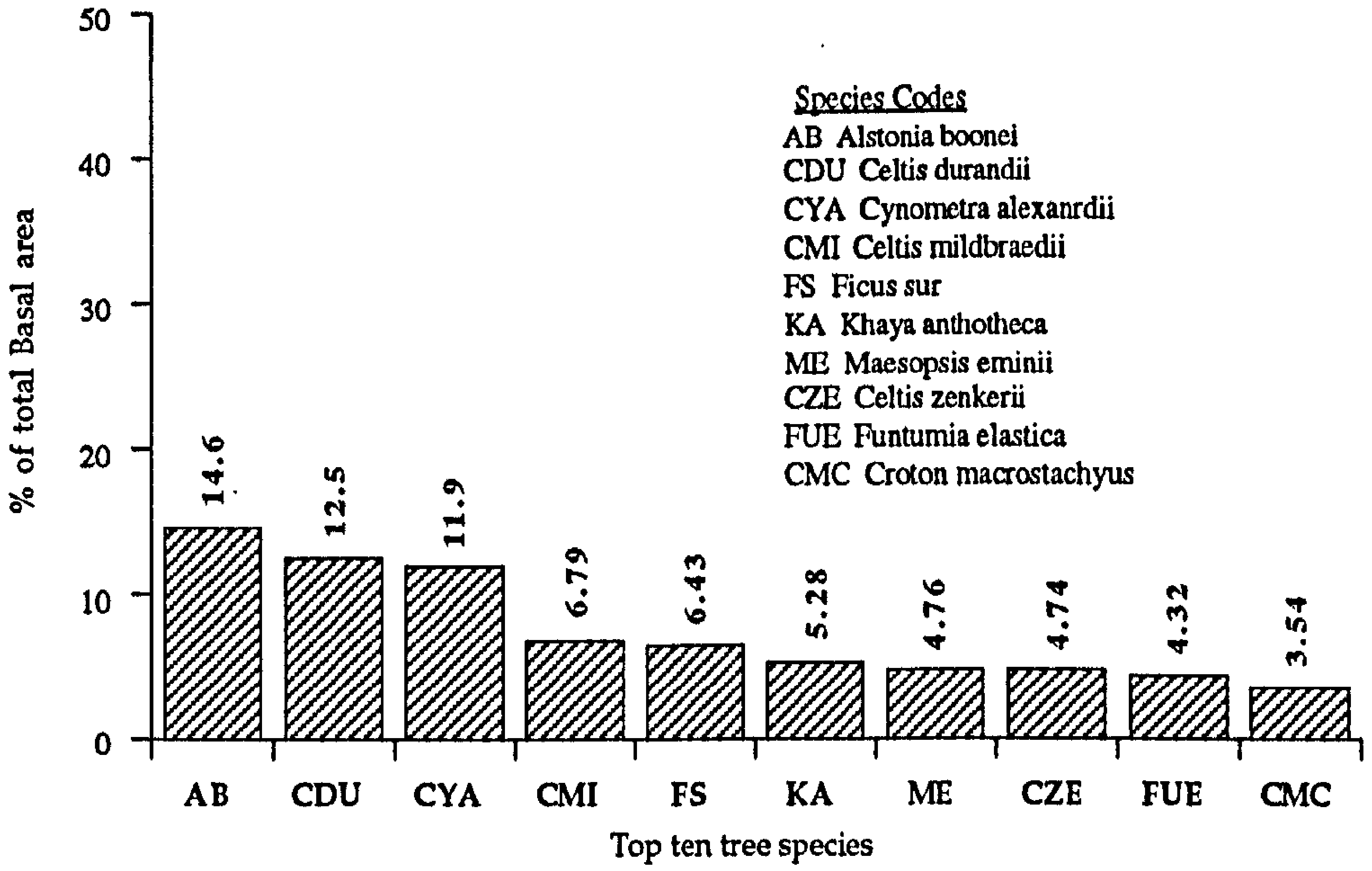


Figure 4.2.a. Proportion of basal area per species for the top ten tree species in N32 home range (logged forest)

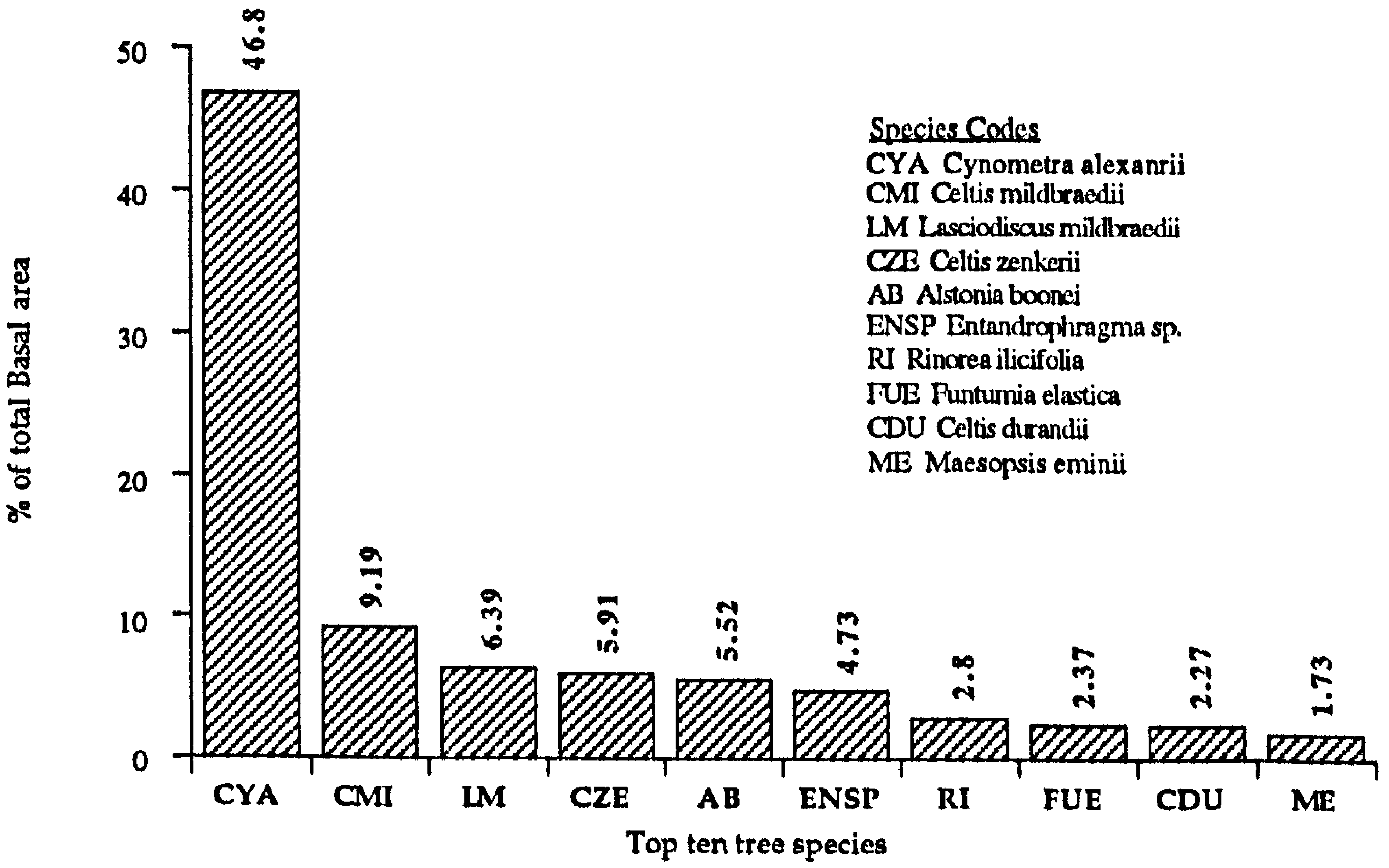


Figure 4.2.b. Proportion of basal area per species for the top ten tree species in N151 home range (unlogged forest)

Stem distribution

Comparing stem frequency distribution in different dbh classes in logged and unlogged forest shows some differences (Figure 4.3). Frequency histograms of stem dbh show a higher proportion of stems at either end of the range of dbh classes in N15 compared to N3. The small dbh classes (0-20m) and the larger dbh classes (81-100;101-120) have a higher proportion of stems in N15. N3 shows a higher proportion of stems in the middle range of dbh classes (21-40, 41-60 and 61-80) compared to N15. The latter difference can be more clearly seen when trees of over 40 cm dbh are considered (Figure 4.4).

Figure 4.3

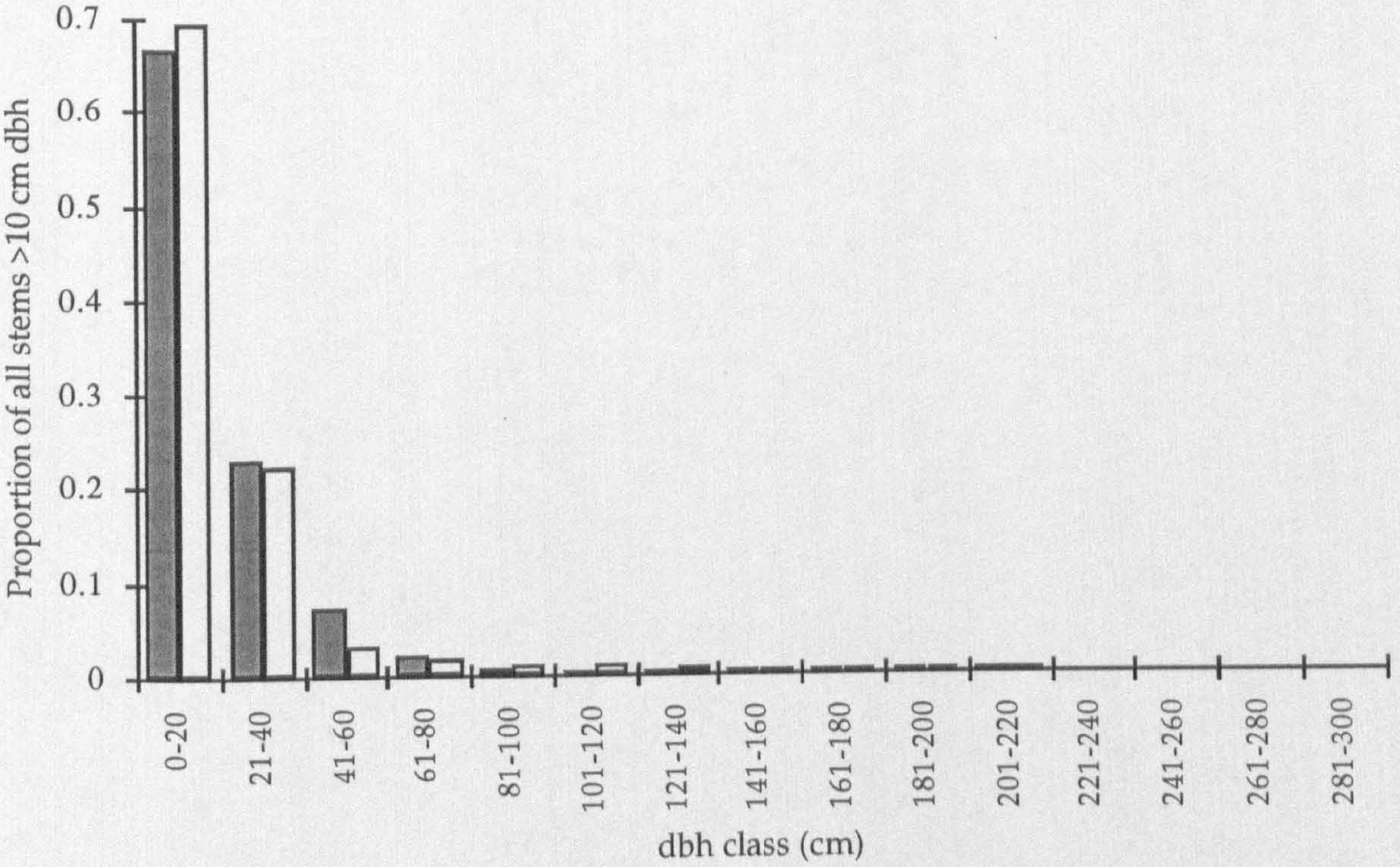


Figure 4.4

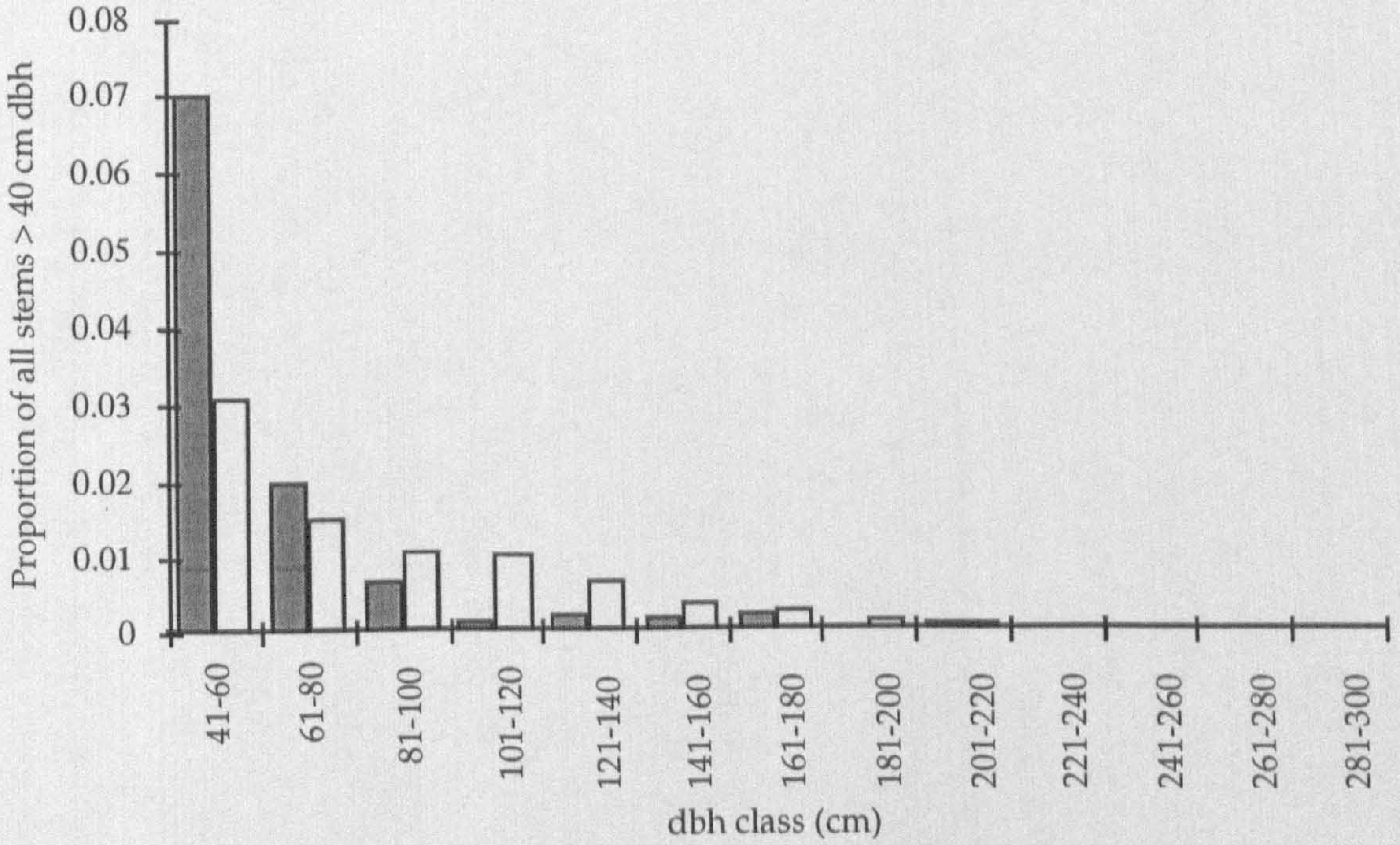


Figure 4.3. and 4.4. Proportion of all stems > 10 cm dbh in 20 cm dbh and >40 cn dbh in different dbh classes for logged and unlogged forest. ■ = N3 (logged) ☐ =N15 (unlogged)

Frequency distribution of stems of *Cynometra alexandri* was compared between logged and unlogged forest. Despite the fact that *Cynometra* was poisoned in N3 and there subsequently appear to be fewer stems in almost all size classes compared to N15, the proportion of small stems (0-20 cm dbh) is much higher in N3. Unlogged forest shows higher proportions of stems in nearly all other dbh classes (Figure 4.5).

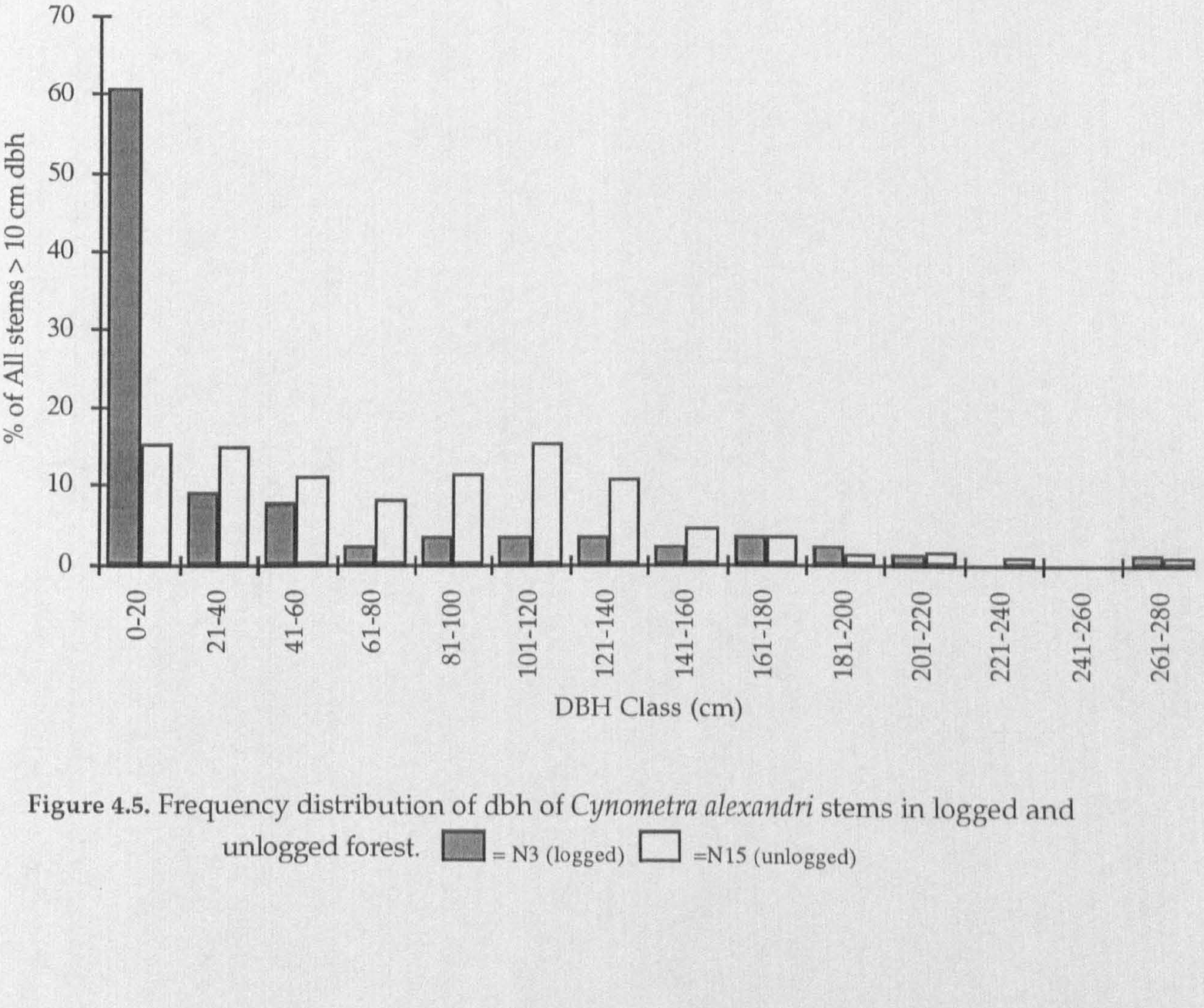


Figure 4.5. Frequency distribution of dbh of *Cynometra alexandri* stems in logged and unlogged forest. ■ = N3 (logged) □ =N15 (unlogged)

Importance Values

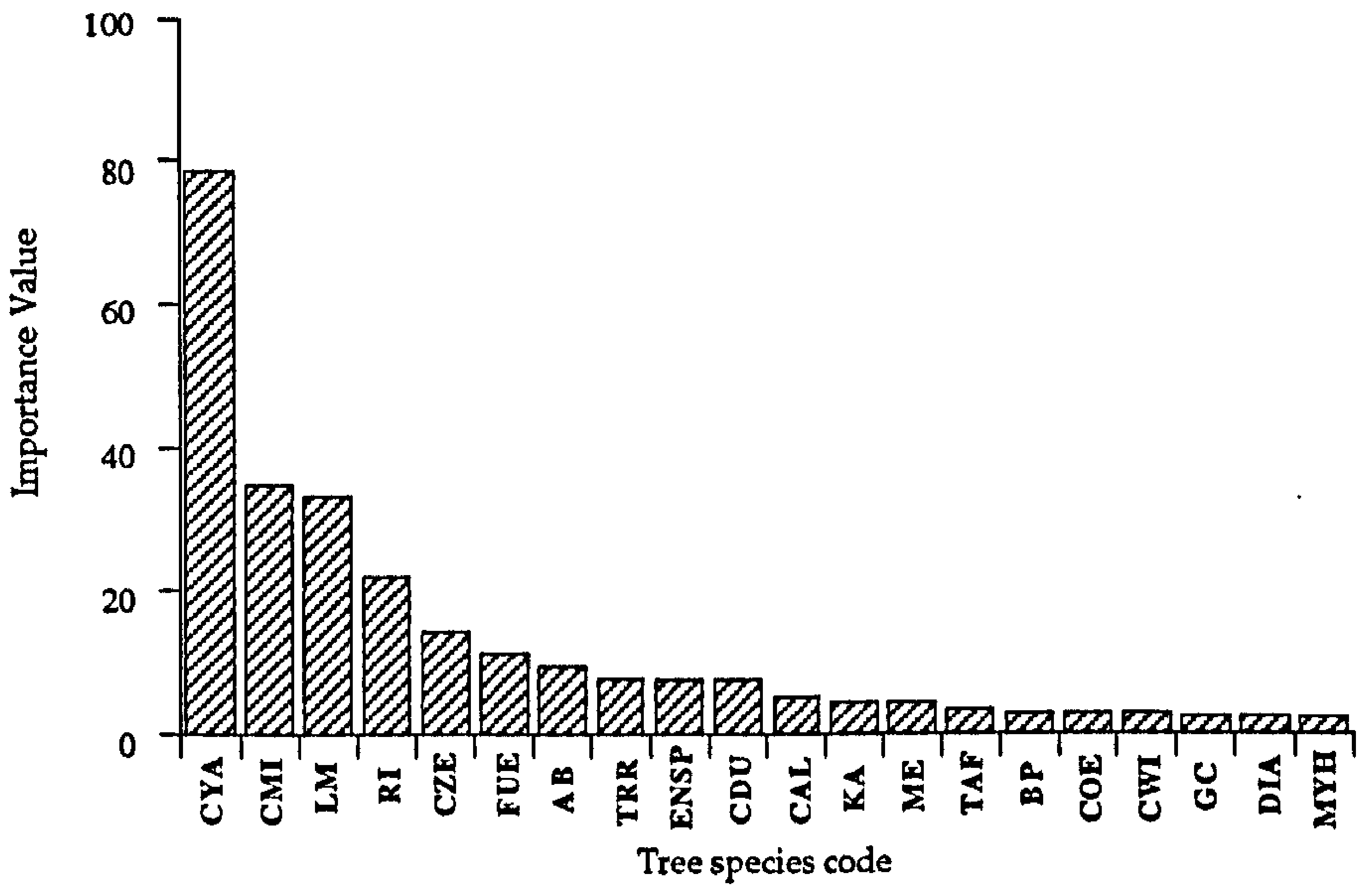
In addition to comparing proportion of basal areas (see above), the top 20 tree species ranked by Importance values were compared for N3 and N15 (Table 4.3 and Figures 4.6.a, 4.6.b).

Table 4.3. Top 20 tree species ranked by Importance value in logged and unlogged forest (Shown graphically in Figures 4.6.a and 4.6.b)

N151: Unlogged				*N32: Logged*			
Rank (rank in N3)	**Species**	**Importance value**	**Code**	**Rank** (rank in N15)	**Species**	**Importance value**	**Code**
1.(5)	*Cynometra.alexandri*	78.68	CYA	1.(2)	*Celtis.mildbraedii*	27.62	CMI
2.(1)	*Celtis.mildbraedii*	34.74	CMI	2.(10)	*Celtis.durandii*	24.91	CDU
3.(11)	*Lasciodiscus.mildbraedii*	33.21	LM.	3.(6)	*Funtumia elastica*	19.20	FUE
4.(15)	*Rinorea ilicifolia*	22.04	RI..	4.(7)	*Alstonia boonei*	18.55	AB
5.(7)	*Celtis.zenkerii*	14.21	CZE	5.(1)	*Cynometra.alexandri*	17.00	CYA
6.(3)	*Funtumia elastica*	11.31	FUE	6.(12)	*Khaya.anthotheca*	14.73	KA
7.(4)	*Alstonia boonei*	9.50	AB.	7.(5)	*Celtis.zenkerii*	14.25	CZE
8.(9)	*Trichilia.rubescens*	7.74	TRR	8.(--)	*Ficus sur*	13.75	FS
9.(--)	*Entandrophragma.sp*	7.65	ENSP	9.(8)	*Trichilia.rubescens*	11.14	TRR
10.(2)	*Celtis.durandii*	7.59	CDU	10.(-)	*Croton macrostachyus*	9.88	CMC
11.(19)	*Chrysophyllum albidum*	5.25	CAL	11.(3)	*Lasciodiscus.mildbraedii*	8.97	LM
12.(6)	*Khaya.anthotheca*	4.57	KA.	12.(13)	*Maesopsis.eminii*	8.86	ME
13.(12)	*Maesopsis.eminii*	4.50	ME.	13.(--)	*Margaritaria discoidea*	8.16	MD
14.(16)	*Tapura fisherii*	3.55	TAF	14.(--)	*Cordia.millenii*	6.34	COM
15.(17)	*Trilepsium madagascarensis*	2.84	BP..	15.(4)	*Rinorea ilicifolia*	5.92	RI
16.(--)	*Coffea eugenoides*	2.83	COE	16.(14)	*Tapura fischerii*	5.21	TAF
17.(--)	*Celtis.wightii*	2.81	CWI	17.(15)	*Trilepsium madagascarensis*	4.62	BP
18.(--)	*Guarea.cedrata*	2.51	GC.	18.(--)	*Ficus.exasperata*	4.39	FE
19.(--)	*Diospyros.abysinnica*	2.48	DIA	19.(11)	*Chrysophyllum albidum*	4.24	CAL
20..(--)	*Myrianthus.arboreus*	2.35	MYH	20.(--)	*Antiaris.toxicaria*	4.23	ANT
Total		260.36				231.97	

As with the comparison by proportion of basal areas, N15 Importance Values are dominated by *Cynometra alexandri* and also feature understorey tree species (*Lasciodiscus mildbraedii* and *Rinorea ilicifolia*) high in the rankings due to their widespread distribution and high stem density (Table 4.3 and Figure 4.5.a). N3 Importance Values show two *Celtis* species ranked highest followed by a large understorey tree species, *Funtumia elastica* , and *Cynometra alexandri* (Table 4.3 and Figure 4.5.b). The total Importance value for the top 20 species is higher in N15 (260.36) compared to N3 (231.97), reflecting the disproportionate density and abundance of fewer species in unlogged forest. This difference is even more marked if only the top 10 species are considered (N15: 226.67 compared to N3:171.03).

a). N151 (unlogged)



b). N32 (logged)

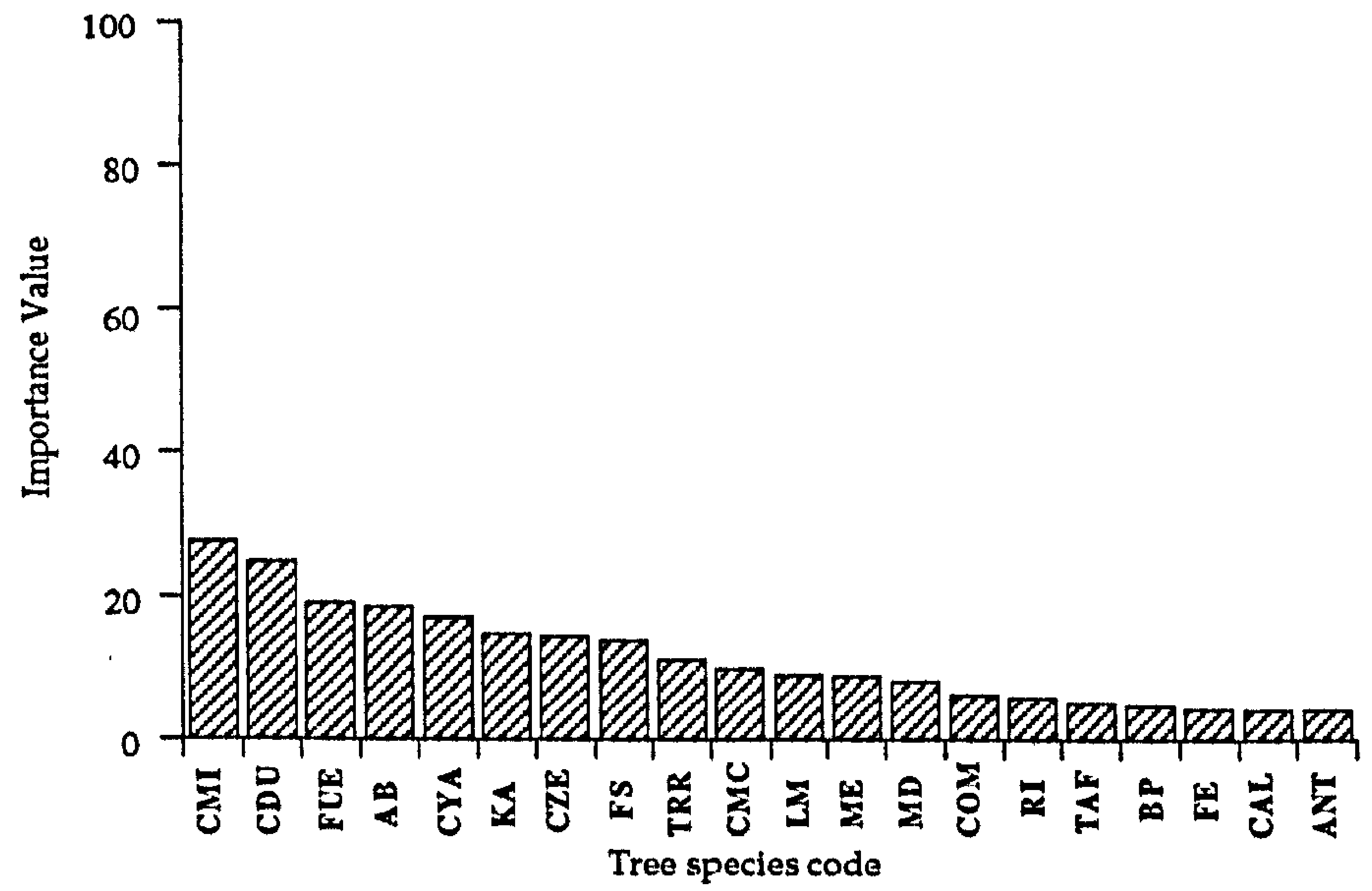


Figure 4.6.a. and 4.6.b. Top twenty species ranked by Importance Values for vegetation in a)N151 and b)N32 group ranges.(For species codes see table 4.3)

If these top 20 tree species ranked by Importance values are classified into broad categories based on forest types (Eggeling 1947a, Synott 1985), there are marked differences between the two compartments. Logged forest shows a higher proportion of 'colonising forest' species whereas unlogged forest is composed mainly of 'mixed forest' and '*Cynometra* -mixed'species (Table 4.4.a.).

Table 4.4.a. Classification by forest type of the top 20 tree species in logged and unlogged forest.

N151: Unlogged			*N32: Logged*		
Rank *(rank in N3)*	*Species*	*Code*	*Rank* *(rank in N15)*	*Species*	*Code*
1.(5)	*Cynometra alexandri*	CYA-M	1.(2)	*Celtis mildbraedii*	M
2.(1)	*Celtis mildbraedii*	M	2.(10)	*Celtis durandii*	COL-M
3.(11)	*Lasciodiscus mildbraedii*	CYA-M	3.(6)	*Funtumia elastica*	COL-M
4.(15)	*Rinorea ilicifolia*	M	4.(7)	*Alstonia boonei*	M
5.(7)	*Celtis zenkerii*	CYA-M	5.(1)	*Cynometra alexandri*	CYA-M
6.(3)	*Funtumia elastica*	COL-M	6.(12)	*Khaya anthotheca*	M
7.(4)	*Alstonia boonei*	M	7.(5)	*Celtis zenkerii*	CYA-M
8.(9)	*Trichilia rubescens*	COL-M	8.(--)	*Ficus sur*	COL-M
9.(--)	*Entandrophragma sp*	CYA-M	9.(8)	*Trichilia rubescens*	COL-M
10.(2)	*Celtis durandii*	COL-M	10.(-)	*Croton macrostachyus*	COL-M
11.(19)	*Chrysophyllum albidum*	M	11.(3)	*Lasciodiscus mildbraedii*	CYA-M
12.(6)	*Khaya anthotheca*	M	12.(13)	*Maesopsis eminii*	COL-M
13.(12)	*Maesopsis eminii*	COL-M	13.(--)	*Margaritaria discoidea*	COL-M
14.(16)	*Tapura fisherii*	M	14.(--)	*Cordia millenii*	COL-M
15.(17)	*Trilepsium madagasc.*	M	15.(4)	*Rinorea ilicifolia*	M
16.(--)	*Coffea eugenoides*	M	16.(14)	*Tapura fischerii*	M
17.(--)	*Celtis wightii*	CYA-M	17.(15)	*Trilepsium madagas.*	M
18.(--)	*Guarea cedrata*	CYA-M	18.(--)	*Ficus exasperata*	COL-M
19.(--)	*Diospyros abysinnica*	CYA-M	19.(11)	*Chrysophyllum albidum*	M
20.(--)	*Myrianthus arboreus*	COL-M	20.(--)	*Antiaris toxicaria*	M

Codes: M=Mixed forest species, COL-M=Colonising-Mixed forest species, CYA-M=*Cynometra*-Mixed forest species.

Comparing the top 20 tree species as classified with forest type (Table 4.4.b) it is clear that logged forest has a higher percentage of colonising-mixed forest tree species compared to unlogged forest (45.98% compared to 12.86%). Some colonising-mixed forest species do occur in unlogged forest, but they do not contribute greatly towards the total Importance Value estimate for the top 20 species (Table 4.4.b). Likewise, some tree species associated with *Cynometra*-Mixed forest do occur in logged forest, but their contribution to the Importance Value estimate is lower than that for unlogged forest (N32: 17.34%, N151: 54.37%). Both areas show similar estimates for Mixed forest tree species, although this figure is higher for logged forest (Table 4.4.b).

Table 4.4.b. Tree species classified by different forest types: number (n) and percentage of Importance Value (%) for the top 20 species

	N32: Logged		*N151:Unlogged*	
	n	%	n	%
M *(Mixed Forest)*	8	36.7	8	32.77
COL-M *(Colonising-Mixed forest)*	9	45.98	5	12.86
CYA-Mixed *(Cynometra-Mixed forest)*	3	17.34	7	54.37

Compartment Comparison

Comparing vegetation data from the two ranges with data for the whole compartments (A. Plumptre unpubl. data), it can be seen that although there are some slight differences in composition and abundance, the vegetation in the two ranges is representative of the respective compartments (N3 and N15). For comparison, data from 200 plots of 0.0154 ha, enumerated in each compartment were used (A.Plumptre unpubl. data.), giving a total area sampled of approximately 3ha. A total of 102 tree species were found in the logged forest compartment (N3) and 83 tree species were found in unlogged forest compartment (N15). These totals are both slightly lower than the totals for the vegetation data in this study (N3 = 113 sp. and N15 = 93 sp.).but this is not surprising given the differences in sampling techniques and size of the total area sampled. Tables 4.5 and 4.6 show the top 10 tree species (ranked by contribution to total stem number per ha and total basal area per ha) for vegetation in the two group ranges and the two compartments.

Table 4.5. Comparison of vegetation data from Group N32 range with data for Compartment N3: top ten species by contribution to stems and Basal area

Stem no./ha		**Basal Area (cm^2/ha)**	
N32 Range (This study)	Compartment N3 (Plumptre unpubl. data)	N32 Range (This study)	Compartment N3 (Plumptre unpubl. data)
1.*Celtis mildbraedii* (102.8)	*Celtis mildbraedii* (87.11)	1.*Celtis durandii* (75060)	*Alstonia boonei* (50401)
2.*Funtumia elastica* (78.44)	*Funtumia elastica* (69.75)	2.*Alstonia boonei* (50408)	*Cynometra alexandri* (33932)
3.*Celtis durandii* (54.0)	*Celtis durandii* (34.73)	3.*Cynometra alexandri* (46780)	*Maesopsis eminii* (32257)
4.*Khaya anthotheca* (38.0)	*Celtis zenkerii* (34.43)	4.*Celtis mildbraedii* (28332)	*Celtis mildbraedii* (29464)
5.*Celtis zenkerii* (35.6)	*Lasciodiscus mildbraedii* (31.73)	5.*Ficus sur* (27092)	*Celtis durandii* (22342)
6.*Trichilia rubescens* (35.5)	*Trichilia rubescens* (23.95)	6.*Khaya anthotheca* (21952)	*Funtumia elastica* (20765)
7.*Lasciodiscus mildb.* (26.0)	*Khaya anthotheca* (15.57)	7.*Maesopsis eminii* (20772)	*Celtis zenkerii* (13778)
8.*Ficus sur* (25.52)	*Cynometra alexandri* (13.17)	8.*Celtis zenkerii* (17748)	*Riciniodendron heud.* (12795)
9.*Croton macrostachyus* (19.6)	*Rinorea ilicifolia* (13.77)	9.*Funtumia elastica* (16912)	*Khaya anthotheca* (11800)
10.*Rinorea ilicifolia* (14.16)	*Croton macrostachyus.* (12.27)	10.*Croton macrostac.* (15500)	*Margaritaria discoidea* (7894)

Table 4.6. Comparison of vegetation data from Group N151 range with data for Compartment N15: top ten species by contribution to stems and Basal area

Stem no./ha		**Basal Area (cm^2/ha)**	
N151Range (This study)	CompartmentN15 (Plumptre unpubl. data)	N151 Range (This study)	Compartment N15 (Plumptre unpubl. data)
1.*Laciodiscus mildbra.* (155,6)	*Lasciodiscus mildbraedii* (125,37)	1.*Cynometra alexandri* (186564)	*Cynometra alexandri* (82340)
2.*Celtis mildbraedii* (146,44)	*Celtis mildbraedii* (97.76)	2.*Celtis mildbraedii* (48832)	*Celtis mildbraedii* (32161)
3.*Rinorea ilicifolia* (100,44)	*Rinorea ilicifolia* (45.15)	3.*Lasciodiscus mildbra.* (35344)	*Alstonia boonei* (31261)
4.*Funtumia elastica* (26.08)	*Trichilia rubescens* (31.83)	4.*Celtis zenkerii* (32572)	*Lasciodiscus mildbraed.* (28220)
5.*Cynometra alexandri* (24.64)	*Cynometra alexandri* (21,11)	5.*Alstonia boonei* (30532)	*Entandrophragma cyl .* (23686)
6.*Celtis zenkerii* (21.32)	*Funtumia elastica* (20.46)	6.*Entandrophragma sp.* (26144)	*Trichilia rubescens* (16489)
7.*Trichilia rubescens* (15.04)	*Celtis zenkerii* (12.34)	7.*Rinorea ilicifolia* (15460)	*Khaya anthotheca* (12412)
8.*Celtis durandii* (9.4)	*Belanophora hypoglauca* (9.09)	8.*Funtumia elastica* (13104)	*Funtumia elastica* (10069)
9.*Chrysophyllum albid.* (4,84)	*Trilepsium madagascarensis* (6,17)	9.*Celtis durandii* (12524)	*Celtis zenkerii* (9741)
10.*Alstonia boonei* (4,56)	*Celtis durandii* (5,85)	10.*Maesopsis eminii* (9580)	*Entandrophragma angol* (9517)

A comparison of vegetation data from the group ranges and the whole compartment (Tables 4.5. and 4.6.) shows broad similarity in terms of species composition and abundance. Basal area estimates are slightly higher in this study partly due to measurement of buttressed trees being carried out in different ways

(Plumptre pers.comm.). Some differences exist between the vegetation in group N32's range as compared to the rest of compartment N3: a higher stem density and basal area of species such as *Ficus sur* and *Celtis durandii* ; lower stem densities of *Cynometra alexandri* and lower basal area of *Maesopsis eminii*.. Species composition and abundance in group N151's range is also very similar to that of compartment N15 with only slight differences being observed eg. higher stem density of one species *Belanophora hypoglauca* in the compartment as a whole or higher basal area of *Celtis durandii* in the range of group N151.

4.4 DISCUSSION

Habitat Composition

Based on the assumption that both areas of forest were similar prior to logging, there are considerable differences observed between the vegetation in N3 compared to N15. This assumption is supported by findings of Plumptre et al (1994) who showed that there were differences in tree communities between the east and the west of the forest, but that neighbouring compartments of the forest were floristically similar. Soils were also shown to be fairly similar (Walaga 1993) and the climate in the two areas is also likely be broadly similar. Therefore the differences observed are likely to be a result of logging.

Differences were observed in species diversity and evenness per plot, but not in mean no. stems or total basal area per plot (basal area is slightly lower in logged forest, but not significantly so). Differences are therefore more in terms of composition and relative abundance than total biomass. Compared to other African forests (Table 4.7), Budongo lies in the mid range of stem densities and species richness estimates. Undoubtedly not as rich as the forests of West Africa or Zaire, Budongo does have a high stem density and species abundance compared to other East African forests such as Kakamega (Table 4.7). The basal area per hectare is also relatively high. That this applies to unlogged forest (N15) as well as logged forest (N3) suggests that logging has the effect of increasing the species diversity of a forest which is already reasonably diverse.

Table 4.7. Comparison of stem density and species richness at some African rainforest research sites.

		Stem density (Per ha)	**Species Abundance**	**Shannon Weiner**
1.Budongo, Uganda.	N3	590.56 (>10 cm dbh)	50 / ha	2.82
	N15	562.68 " "	38 / ha	2.00
2.Kibale, Uganda.	Kanya.	268 (>10 cm dbh)	42 /1.55 ha	2.79
	Ngogo	404 " "	52 /1.55 ha	2.76
3.Kakamega, Kenya.		89.76 (>20 cm dbh)	62 /21.78 ha	3.45
4.Mungamba,	logged	---	81/1.5 ha	---
Zaire	unlogged	---	106/1.5 ha	---
5.Lope, Gabon.		404 >10 cm dbh)	110 /1.25 ha	---
6.Tiwai, Sierra Leone.		1116 (>5cm dbh)	133 /0.56 ha	---

References
1.This study, 2. Butynski (1990), 3. Cords (1987), 4. Hall (Unpubl.), 5. White (1994a), 6. Oates et al. (1990).

Basal Area and Stem Distribution

The reduction in basal area attributed to logging - 6.96% -is less than reported for other sites (Table 4.8, Skorupa 1986, White 1992, 1994a) where measurements were taken sooner after logging. In a relatively long period post logging (almost 45 years), N3 may have attained a basal area total approaching that of unlogged forest. Despite their removal during felling, stems of *Khaya anthotheca, Alstonia boonei, Maesopsis eminii* and other timber trees are still present in N3, often with higher Importance values than observed in N15, indicating some recruitment/regeneration of timber species.

Table 4.8. Comparison of felling intensities and % change in Basal Area at different logging sites

Site	*Author* *Years since logging*	*Felling intensity*	*Vol /ha(m^3)*	*Change in Basal Area*
Sungai Tekam Malaysia	Johns (1986) 0 years	18	---	50.9 % Reduction (Stems>30 cm dbh)
West Kalimantan, Indonesia	Cannon et al (1994) 8 years	10.6	---	45% Reduction
Para state Brazil	Uhl and Vieira (1989) 25 years	4-8	52	43% Reduction (Stems>10 cm dbh)
Amazonas state Brazil	Johns (1991) 10 years	3-5	---	57.42%
Tailandia Brazil	Uhl et al (1991) 25 years	2	16	55% Reduction (Stems>10 cm dbh)
Morondava Madagascar	Ganzhorn et al (1990) 12 years	---	10	Reduction
Lope, Gabon	White (1994a) 8 years	2	---	10-13% Reduction
Mungamba, Zaire	Hall (Unpubl.) no date given	---	---	14.6 %/21 % Reduction Immediately post logging/ 12 yrs post logging
Kibale	Skorupa (1986) 15 years	---	14/21	25%/50% Reduction (Light/Heavy)
Budongo	This study 47 years	~3	80 (33.02)*	6.96 % Reduction

* A range of felling intensities was carried out through the various compartments in Budongo, the Mean vol removed per hectare was 33.02 m^3/ha (n=43, SD=18.46, Range = 8.1m^3/ha to 94m^3/ha). Compartment N3, the logged compartment used in this study, experienced one of the highest felling intensities of 80 m^3/ha.

Hall (Unpubl.), in forest floristically very similar to Budongo found a lower basal area and total species number in logged forest compared to unlogged forest. He documented basal areas of 32.13m^2/ha, 34.56m^2/ha and 40.49m^2 /ha in similar forest types for forest logged 12yrs previous, forest recently logged and unlogged forest in Zaire. This constituted a reduction in basal area of around 14.6 % for forest immediately post logging and 21% for forest 10 years post logging. Both the logged and unlogged sites in Mungamba were more species rich than either N3 or N15 (Table 4.7) which may account for the difference in response to logging. There may also have been a higher felling intensity for this site[not indicated in Hall (Unpubl.)] or other site specific differences which account for the different response. Large reductions in basal area have been reported for some sites where felling intensities were higher and more damage caused during felling (Table 4.7).

Stem distribution in dbh classes differs between N3 and N15, with a higher proportion of stems in the small and large size classes in unlogged forest while logged forest shows a higher proportion in the mid range of size classes. As expected for lowland tropical rainforest, both N3 and N15 show a reverse 'J' curve for stem distribution among size classes. The incidence of treefall gaps (includes branch falls) is slightly higher in logged forest as are liane tangles in tree canopies. Both of these effects are characteristic of logged and indeed other 'disturbed' forest sites (Kasenene and Murphy 1991) and may be one of the factors which leads to an increase in preferred habitat for some species of primates (Thomas 1991). It is possible that many lianes, especially 'light loving' species will experience enhanced growth conditions in logged forest (Johns 1988a). As a generalist species, blue monkeys may make use of gap edges and heavy liane growth as areas of high food availability and preferred resting sites (pers. obs).

Importance Values

Importance Values incorporate measures of stem density, frequency and basal area and present an overall view of the forest. Unlogged forest is dominated by few common species which contribute greatly to the basal area and occur at high stem density while logged forest has a much more even distribution of the total basal area and stem number among species. The top 20 tree species (ranked by Importance Value) in logged forest can be classified mainly as Colonising-Mixed forest or Mixed-Forest species with only a few *Cynometra*-Mixed forest species. In unlogged forest, the majority of tree species can be classified as Cynometra-Mixed forest species and Mixed forest species. Colonising-Mixed forest species do occur in unlogged forest, but make a very small contribution to the Importance value estimate for the top 20 species.

The unlogged forest is also fairly typical of mono-dominant forests in the tropics (Connell and Lowman 1989, Hart et al. 1989, Hart 1990) where commonly between 50 to 100% of the canopy consists of one tree species. Hart et al (1989) describe the *Cynometra* dominated forest in Budongo as 'a self replacing climax type monodominant' while Connell and Lowman (1989) use the description 'persistent dominant'. These classifications reflect the ability of *Cynometra* to maintain dominance by recruiting large numbers of seedlings under it's heavy shading canopy (Hart 1995), a strategy reported for other monodominant species (Kachi et al 1993). The frequency distribution of *Cynometra* stems in different dbh size classes in N15 shows that recruitment of seedlings is high. However, there also appears to be a high recruitment rate of *Cynometra* seedlings in N3 despite the heavy poisoning carried out post-logging and the lack of apparent *Cynometra* dominance.

Compartment Comparison

Comparing the vegetation data from group ranges with the data for the whole compartment (Plumptre unpubl. data), it is clear that the vegetation in group ranges is representative of the whole compartment. On closer examination, some subtle differences are detected. N32's range may not be entirely typical of the whole compartment due to its high Figure density and slight difference in species composition. The range of group N151 appears to have a high density of *Celtis durandii* compared to the rest of the compartment. However, differences are not substantial and sampling techniques also differed with respect to size of plots and the total area sampled. Plumptre (unpubl. data) used many small plots distributed over a larger area (the whole compartment) resulting in a smaller total area sampled compared to this study. Some species may also be distributed locally giving rise to differences between group ranges and the whole compartment. This observation highlights the importance of representative habitat sampling when investigating the effects of logging on primates and other wildlife.

Conclusions

i) There are distinct differences between logged and unlogged forest in terms of species diversity and relative abundance. Logged forest has a significantly higher tree species diversity per unit area and a more even distribution of basal area and

Importance values across all species. There are no significant differences in terms of total Basal area or stem number although logged forest has a lower Basal area (6.96 %) and more stems per unit area.

ii) Unlogged forest shows a high frequency of tree species associated with Mixed or *Cynometra*-mixed forest types, individuals of these species showing a high frequency of stems in the large and small size classes. Logged forest by contrast shows a high frequency of species associated with mixed or Colonising-mixed forest types and individuals show a higher frequency of stems in the mid size classes.

iii) It is likely that vegetation in the two group ranges is representative of the vegetation within the whole compartments and that the differences observed between N3 and N15 are largely as a result of logging.

CHAPTER 5

PHENOLOGY PATTERNS AND FOOD AVAILABILITY

5.1 INTRODUCTION

In most lowland tropical rainforests, there is some seasonal variation in the phenological patterns of tree species during an annual cycle (Chapman et al. 1994, Leighton and Leighton 1983, Lieberman and Lieberman 1986). Previous studies of plant part production in forest trees have documented seasonality of production of leaves, fruits and flowers (see van Schaik et al 1993 for a review). Factors including temperature, rainfall, humidity levels and daylength may be important in determining such patterns (Kinnaird 1992, Longman and Jenik 1987, Tutin and Fernandez 1993, White 1994c). There has been considerable discussion regarding the methodological problems of estimating plant part production accurately (see Chapman et al 1992 for a review), and it is important to standardise methods to allow inter-site comparisons.

These seasonal patterns may also show within habitat differences in timing and amplitude between logged and unlogged forest sites or disturbed/undisturbed forest (Burghouts et al. 1992, Burghouts et al. 1994, Johns 1985, Rodman 1978, van Schaik 1985, van Schaik et al. 1993). Changes in canopy structure following logging may lead to variation in light levels or other climatic variables. If logging affects the size class distribution, there may be a change in phenological production as a result. Finally, tree species with different growth strategies which become more common as a result of logging may influence the seasonal patterns of plant part production (Rodman 1978).

Burghouts et al. (1994) reported a much more patchy leaf fall in unlogged forest compared to logged forest, and Fimbel (1994) found differences in seasonal patterns of leaf and fruit production between old forest and secondary re growth. Van Schaik (1986) reported distinctly different patterns of plant part production in mature and young forest in Sumatra. The responses of primates to changes in seasonal plant part production are not fully understood and few studies have addressed this issue in the context of logging. As well as responding to changes in vegetation structure and composition, primates may show differences in diet and ranging patterns due to differences in seasonal production patterns between logged and unlogged forest (Leighton and Leighton 1986, Newton 1988, van Schaik et al 1993). Quantifying seasonal food availability in logged and unlogged forest may highlight differences important in the context of range use and dietary composition (Peres 1994).

5.2 METHODS

A total of 632 individuals of 24 species were sampled during 16 months (32 two week phenology periods), but data presented here apply only to the 12 month period (24 two week samples) when dawn to dusk follows were carried out. Scores from phenology trails and phenology plots were combined for tree species in N3 and N15. Using a two week interval for phenology estimates (Chapter 3), although more labour intensive, probably gives a more accurate estimate of production. Some trees were observed to start and finish the phenophase for certain items well within the two week period - sampling by monthly intervals would fail to record these events. An overview of the broad phenological patterns can be given by summing the production scores for all tree species (both compartments combined) for each two week sample period. For further comparative analyses, data for the 15 species which occurred in both compartments were used. To compare seasonal patterns of phenological production in the two compartments, item production scores were summed (all individuals of each species) and then divided by the total basal area for that species. This gives a score which expresses the production of items per unit of basal area (cm^2) for each tree species. Scores for each item were compared over the 24 two week periods using a Wilcoxon rank sum test.

To compare estimated availability of food items throughout the year, phenology production scores were then multiplied by the mean basal area per plot for each tree species (estimates for the 15 shared species from vegetation plot data: Chapter 4). This gives a comparable estimate of food item availability for two of the four ranges. This calculation assumes a constant relationship between basal area and plant part production at least for the individuals of the same species which are being compared (sensu Chapman 1988). This assumption is probably true for individuals of the same species in the two areas although different species will show different relationships.

Finally, for calculation of Selection Indices (See Chapter 7), phenology production scores for each two week period were multiplied by the proportion of basal area for each tree species to give an index of proportional availability for food items within each range.

The number of individuals of each species sampled varied according to the abundance of the tree species (Table 5.1) but all species which featured prominently in the diet were well represented by the sample (See Chapter 7).

Table 5.1. Tree species and numbers of individuals included in phenology sampling.

	N3	N15	Total	Present in both areas.
Albizzia sp.	6	0	6	
Alstonia boonei	18	22	40	*
Antiaris toxicaria	5	0	5	
Celtis durandii	50	24	74	*
Celtis mildbraedii	24	51	75	*
Celtis zenkerii	18	30	48	*
Chrysophyllum albidum	16	16	32	*
Chrysophyllum perpulchrum	4	14	18	*
Cleistopholis patens	2	1	3	*
Cordia milleni	12	4	16	*
Croton macrostachyus	24	4	28	*
Cynometra alexandri	22	48	70	*
Entandrophragma sp.	3	17	20	*
Ficus exasperata	16	0	16	
Ficus mucoso	3	0	3	
Ficus sansibarica	1	0	1	
Ficus sur	16	0	16	
Funtumia elastica	20	22	42	*
Holoptelea grandis	6	3	9	
Khaya anthotheca	21	9	30	*
Lasciodiscus mildbraedii	3	8	11	
Maesopsis eminii	42	14	56	*
Mildbraedeodendron excelsum	0	5	5	
Morus lactea	6	2	8	*
	338	**294**	**632**	**560**

* Species important in the diet and occurring in both areas were used to compare seasonal production in the two compartments (see below).

Overall Patterns Of Production

Comparing the seasonal patterns of production for logged and unlogged areas combined, it can be seen that production of plant parts is distinctly seasonal and may be related to rainfall patterns (Figures 5.1a to 5.1d). It seems therefore that the food items of all groups are patchily available in time and fluctuate throughout the year.

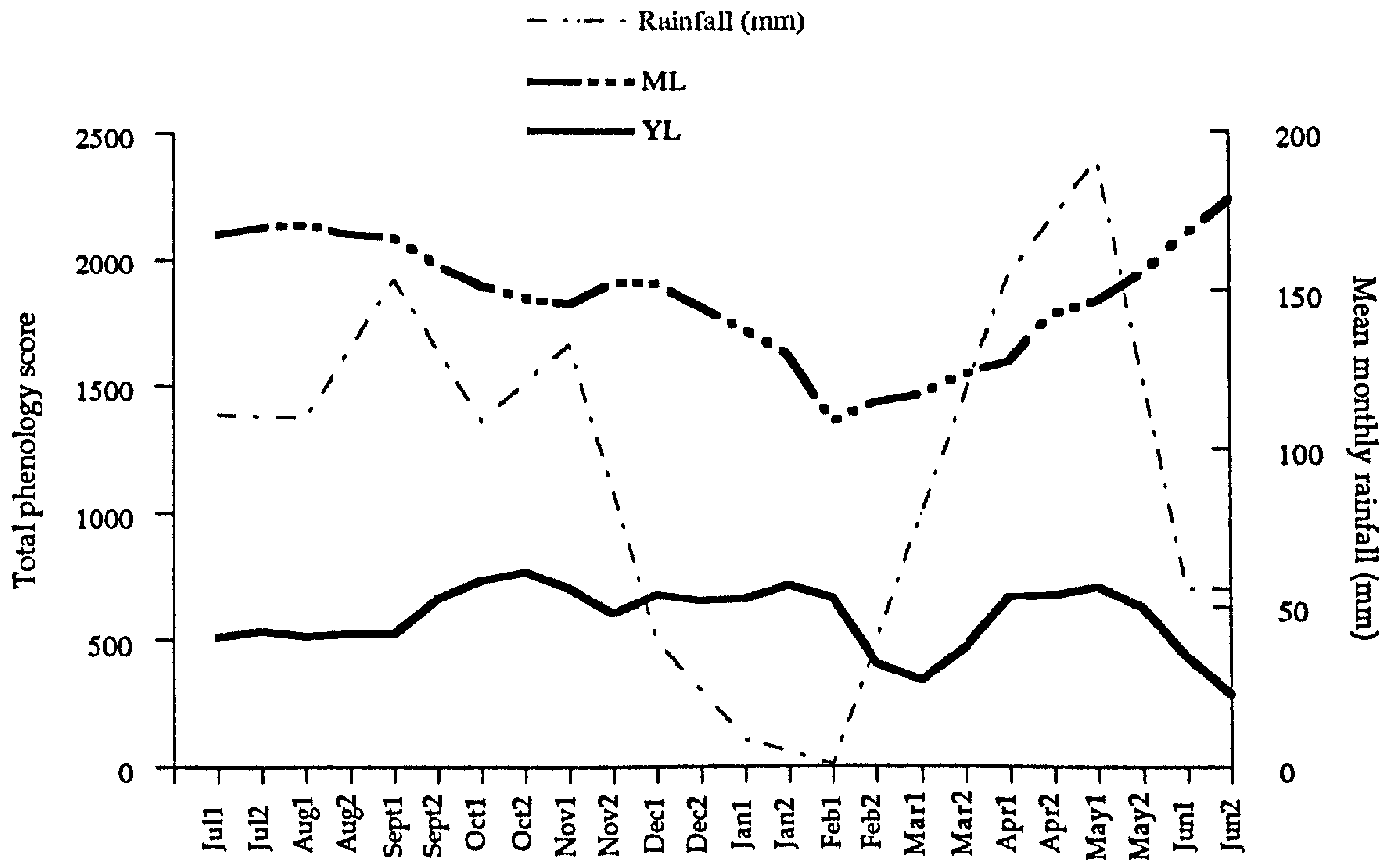


Figure 5.1.a. Seasonal production of mature leaves (ML) and young leaves (YL) in both compartments combined (all tree species)

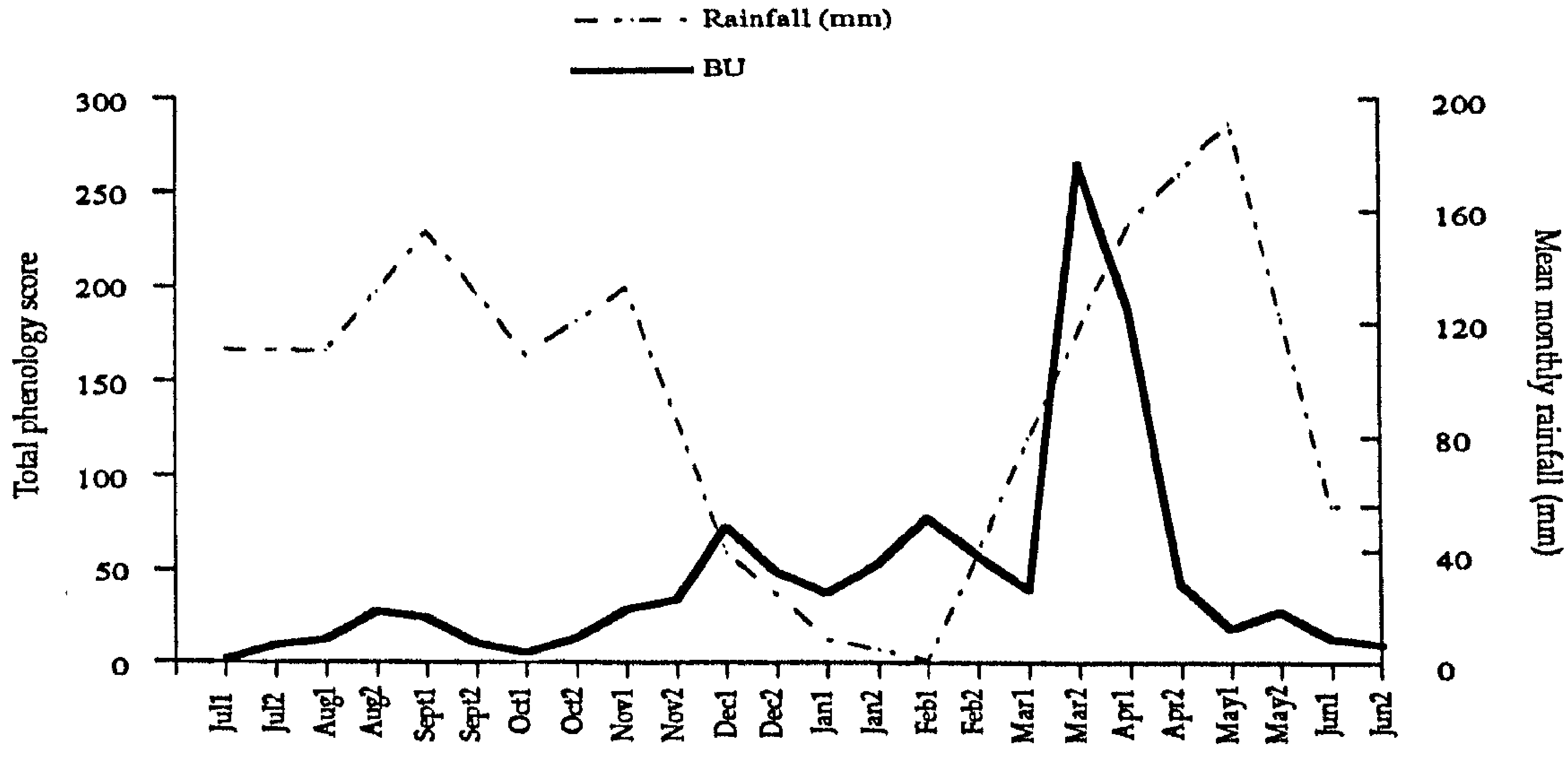


Figure 5.1.b. Seasonal production of leaf buds (BU) in both compartments (all tree species)

Mature leaf production throughout the year shows a fairly predictable pattern, reaching a minimum during the long dry season (January-March). Following a peak in young leaf production the abundance of mature leaves then increases through April-May back to its former level by June (Figure 5.1a). Young leaf production shows two noticeable peaks, both occurring during the rainy seasons (September-November) and (March-May). The latter represents a period of leaf flushing after widespread shedding of leaves during the dry season. The other peak (Sept-Nov together with other increases in young leaf production represent continuous flushing of young leaves as mature leaves are replaced throughout the annual cycle. Reductions in young leaf production are observed at the end of the long dry season (February-March) and during the short dry season (June-August)(Figure 5.1a). Bud production occurs throughout the year but with a definite peak in March-April, prior to and during the production of young leaves (Figure 5.1.b).

As with leaf production, fruit production in the two compartments shows strong seasonality (Figure 5.1.c). The two observed peaks in ripe fruit production correspond fairly closely with the two rainy periods: September-November and late February-late April. Unripe fruit production shows a negative correlation with ripe fruit production and occurs throughout the dry seasons - December-February and May-August - just prior to the onset of rain. Ripe fruit production then commences with the onset of rain and decreases during the drier periods. Flower production (Figure 5.1.d) again shows bi-modal peaks, occurring at the start of the long dry season (December) and the end of the long dry season (March-May). This latter peak in flower production, together with unripe fruit production, may be triggered by drought during the long dry season (December-March).

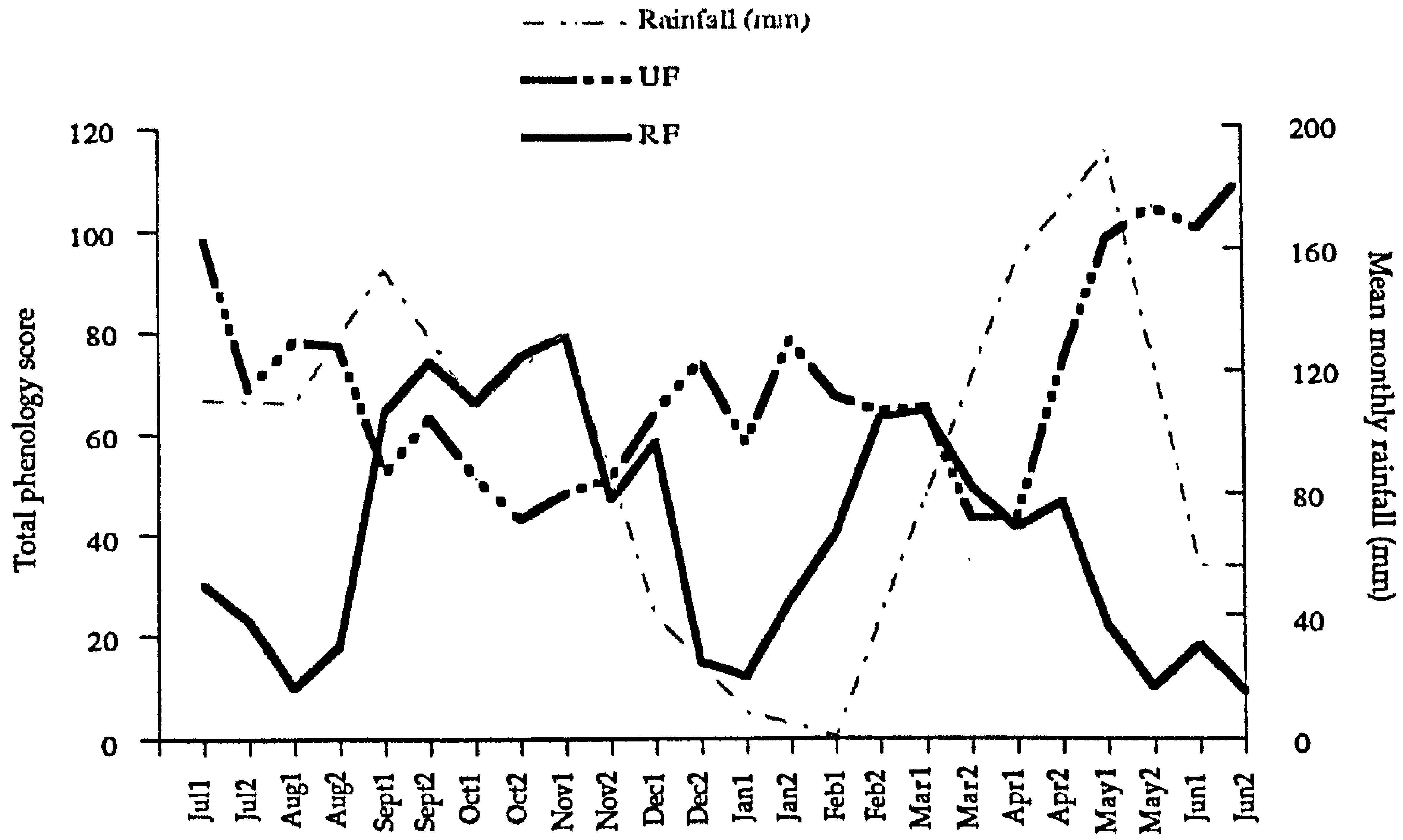


Figure 5.1.c. Seasonal production of ripe (RF) and unripe fruit (UF) in both compartments (all tree species)

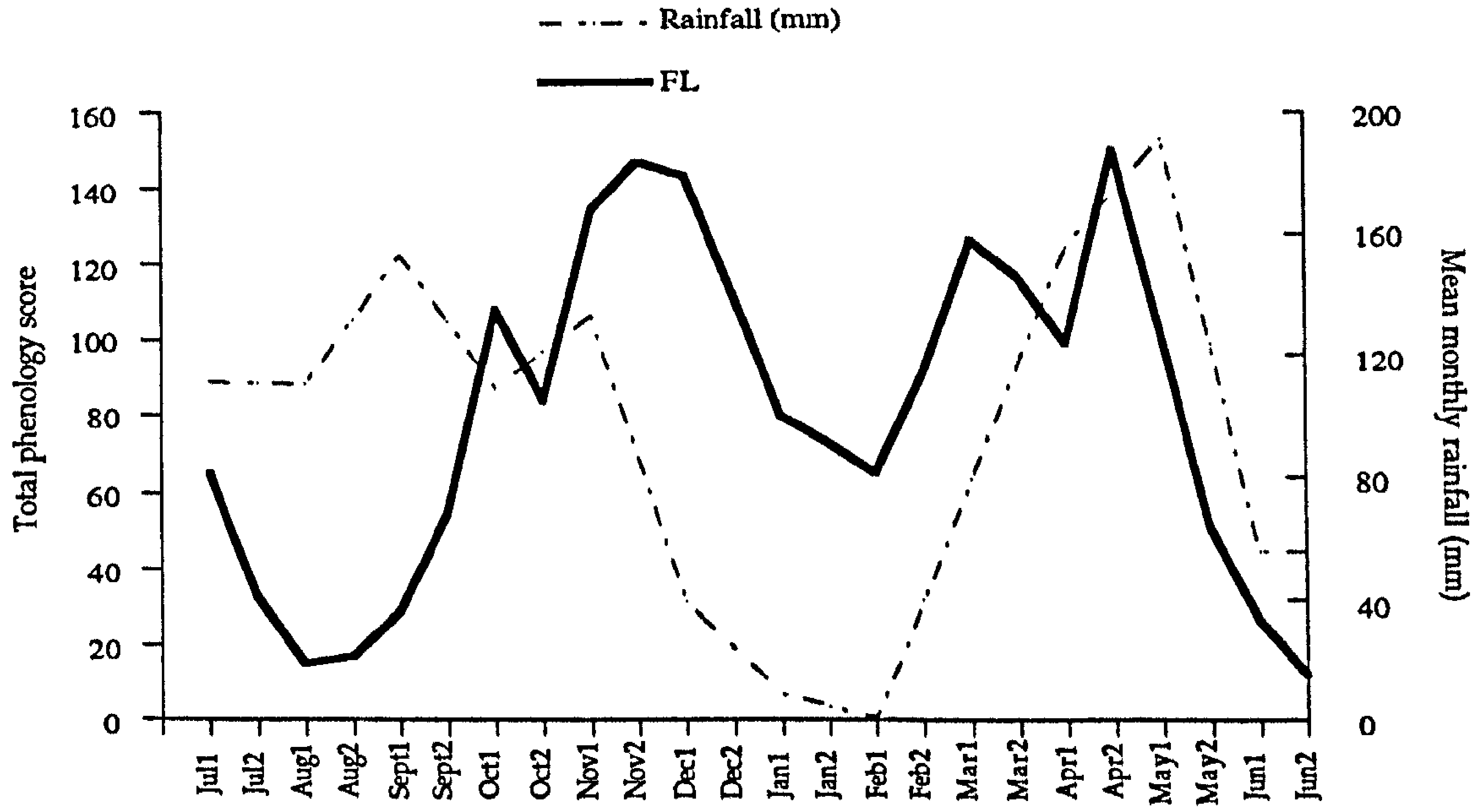


Figure 5.1.d. Seasonal production of flowers (FL) in both compartments (all tree species)

Comparison Between N3 And N15

Of the 24 tree species included in phenology sampling, 15 occurred in both areas therefore comparison of seasonal production and availability of food items was restricted to these 15 species. The items from these 15 tree species represented 60.33% and 73.50% of all food items for groups N32 and N31; 67.76% and 67.4% of all food items for groups N151 and N152 (see Chapter 7). Therefore, although the suite of species does not cover the whole dietary spectrum, these estimates of production will give a reasonable indication of production of the main dietary items. Using production scores per unit basal area for the 15 tree species which occurred in both compartments the seasonal patterns of production are compared in Figures 5.2.a to 5.2.d Tree species in logged and unlogged forest show broadly similar patterns of production although some differences in seasonal timing are observed (see below).

Testing seasonal production scores (per unit of basal area) between N3 and N15 shows no significant differences by Wilcoxon rank test for all items (Table 5.2).

Table 5.2. Wilcoxon z values and Probabilities for tests between production scores for N3 and N15 (15 shared sp).

N3/N15 Category	z	P
Ripe fruit	1.143	ns, P>0.1
Unripe fruit	0.143	ns, P>0.1
Mature Leaves	0.200	ns, P>0.1
Young Leaves	1.57	ns, P>0.1
Buds	0.286	ns, P>0.1
Flowers	0.571	ns, P>0.1

Scores were then compared for dry season (<75mm rainfall: Jun1-Jul2 and Nov2-Mar1) and wet season (>75mm rainfall: Aug1-Nov1 and Mar2-May2). Mature leaf production patterns were similar in logged and unlogged forest and did not show significant differences (Table 5.2.a, Figure 5.2a). There are however some differences in the timing of production of unripe fruit and young leaves (Table 5.2a). Unripe fruit and young leaf production are significantly higher in the wet periods in logged forest (Table 5.2a, Figures 5.2a, 5.2.c). Bud production appears to show larger, more concentrated peaks in unlogged forest during the dry season, indicating more synchronous bud 'flushing', while bud production is higher in the wet season in logged forest. However, these differences are not significant between logged and unlogged forest (Table 5.2a, Figure 5.2.b). . Flower production occurs in two peaks in both logged and unlogged forest, these peaks are slightly later in unlogged forest (Figure 5.2.d), but there are no significant differences.

Table 5.2a Wilcoxon Rank test between logged and unlogged forest for wet and dry season plant part production scores

	Z Values N3/N15			
	Dry		Wet	
Ripe fruit	0,667	ns, $P>0.1$	1,177	ns, $P>0.1$
Unripe fruit	1,726	ns, $P>0.1$	2,71	* $P<0.05$ (N3 > N15)
Mature Leaves	0,235	ns, $P>0.1$	0,863	ns, $P>0.1$
Young Leaves	0,157	ns, $P>0.1$	2,67	* $P<0.05$ (N3 > N15)
Buds	1,138	ns, $P>0.1$	0,392	ns, $P>0.1$
Flowers	0,157	ns, $P>0.1$	0,549	ns, $P>0.1$

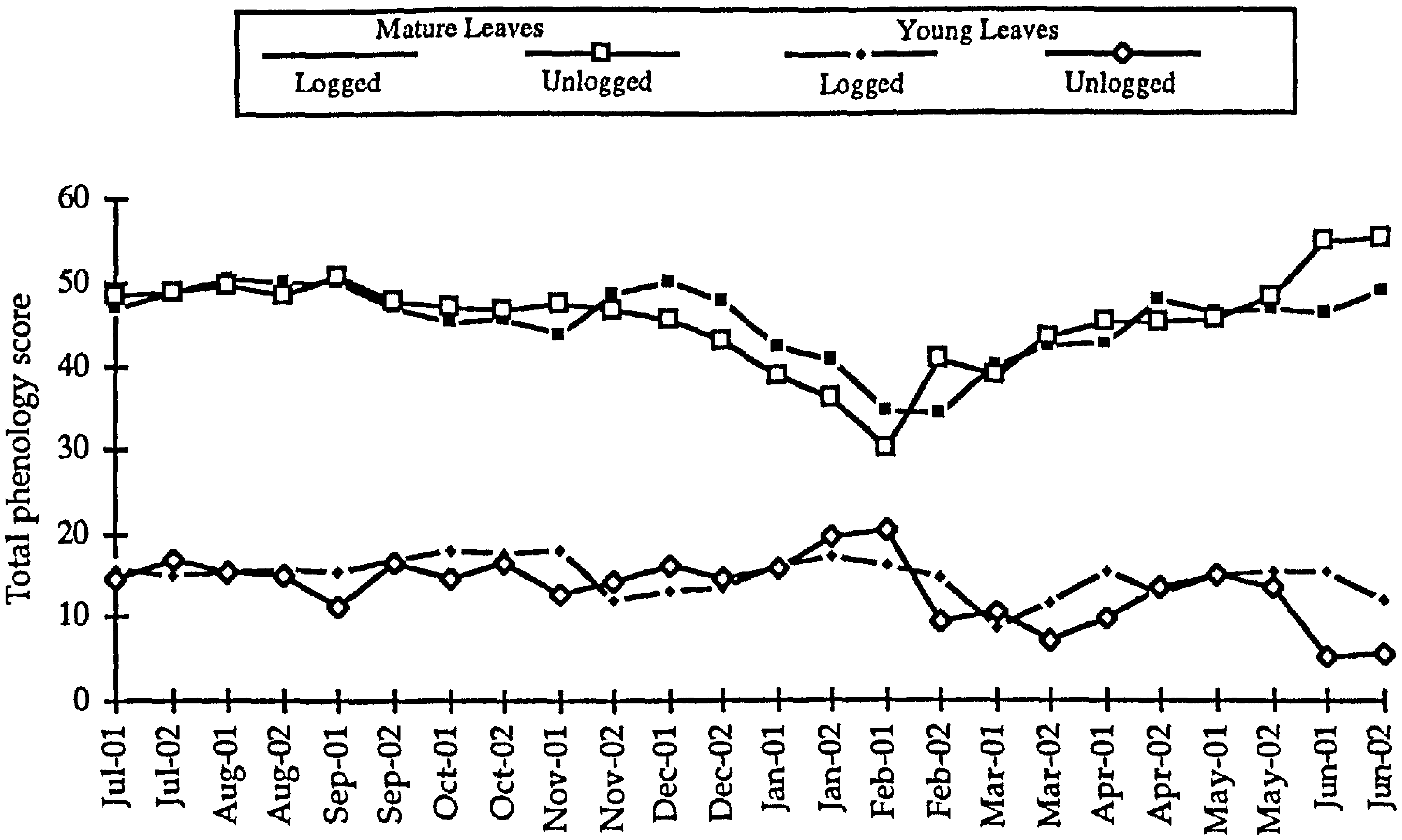


Figure 5.2.a. Comparison of mature leaf and young leaf production between common tree food species in logged and unlogged forest (15 species)

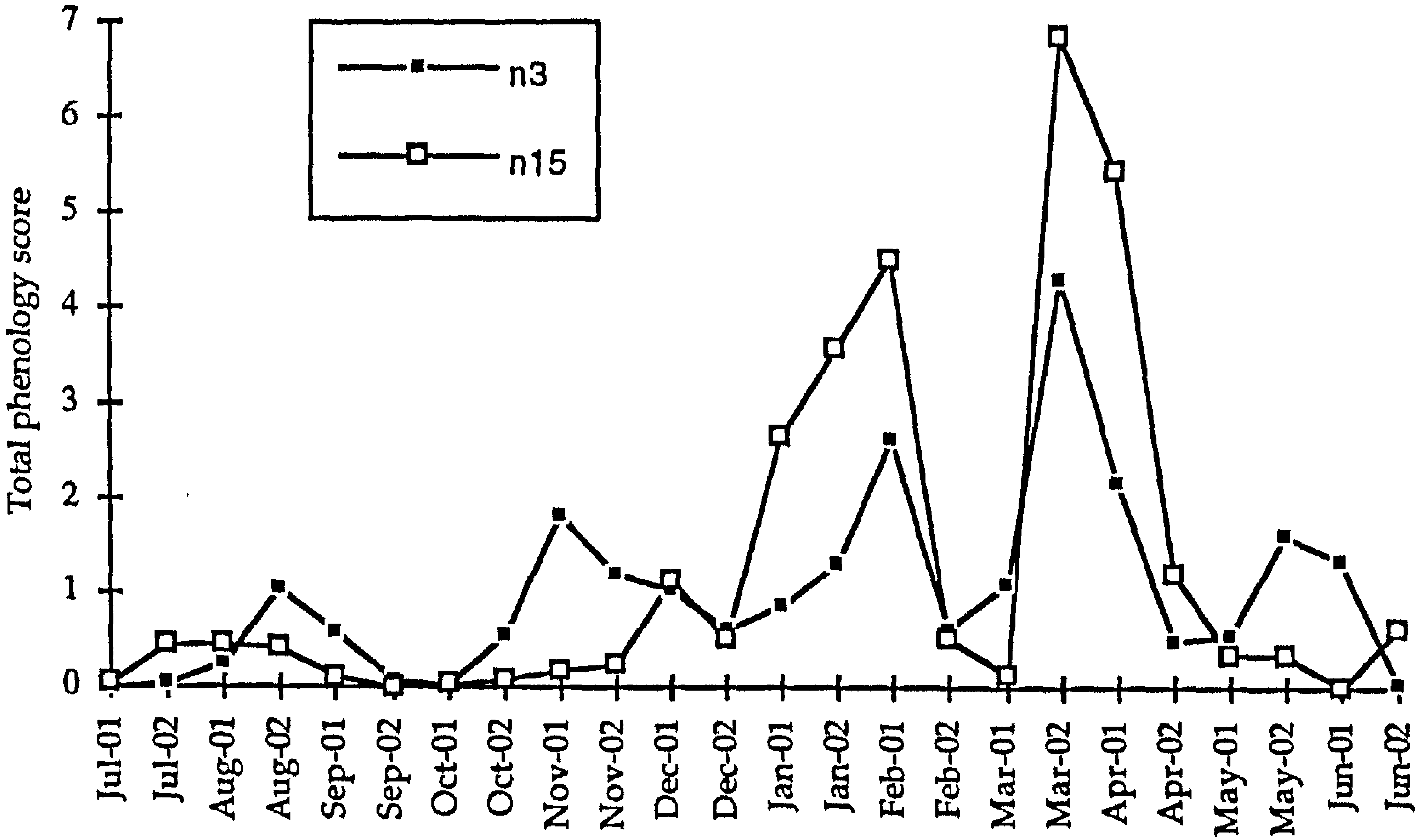


Figure 5.2.b. Seasonal leaf bud production in logged (N3) and unlogged (N15) forest (15 species combined)

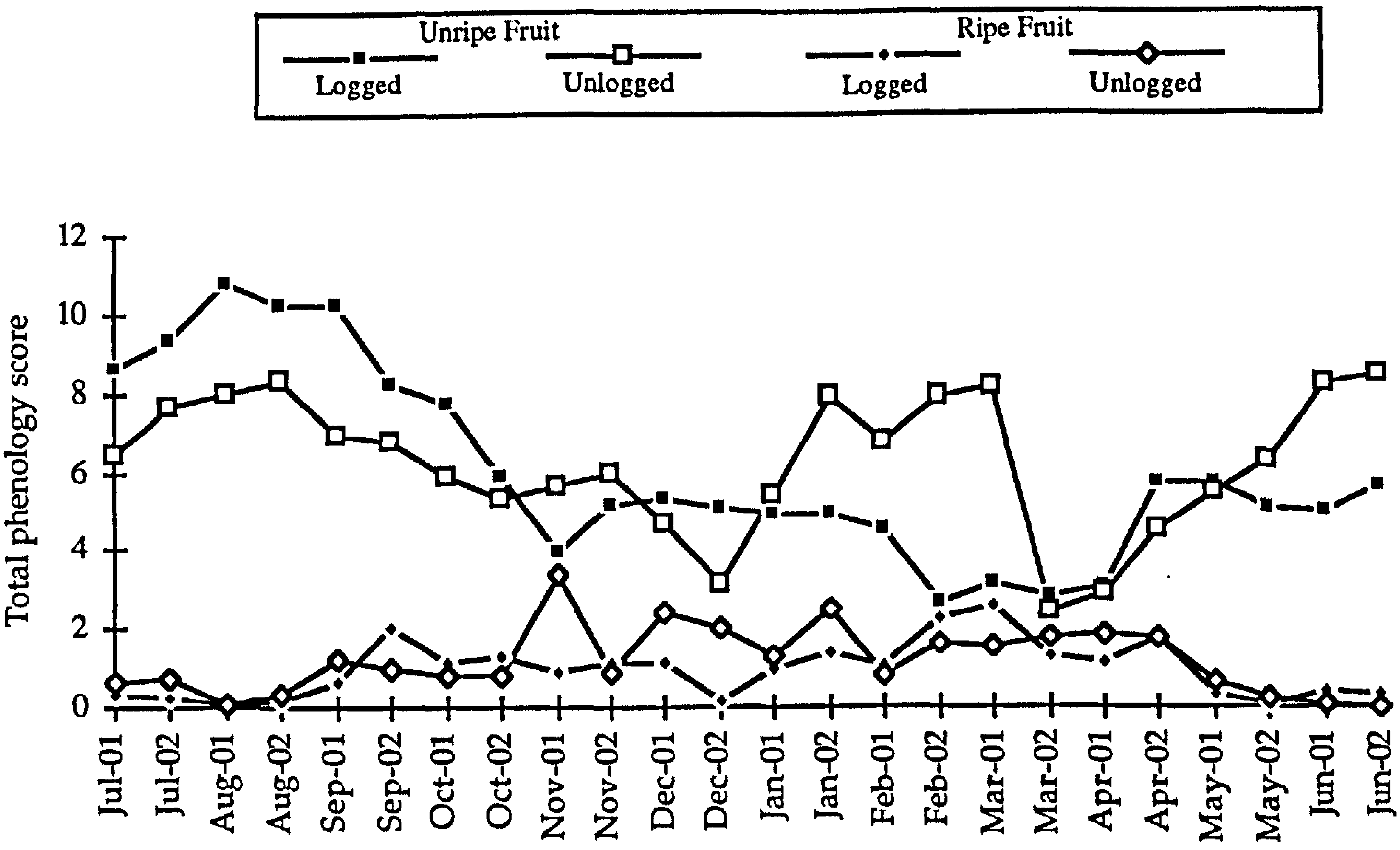


Figure 5.2.c. Ripe fruit and unripe fruit production in logged and unlogged forest.(15 species combined)

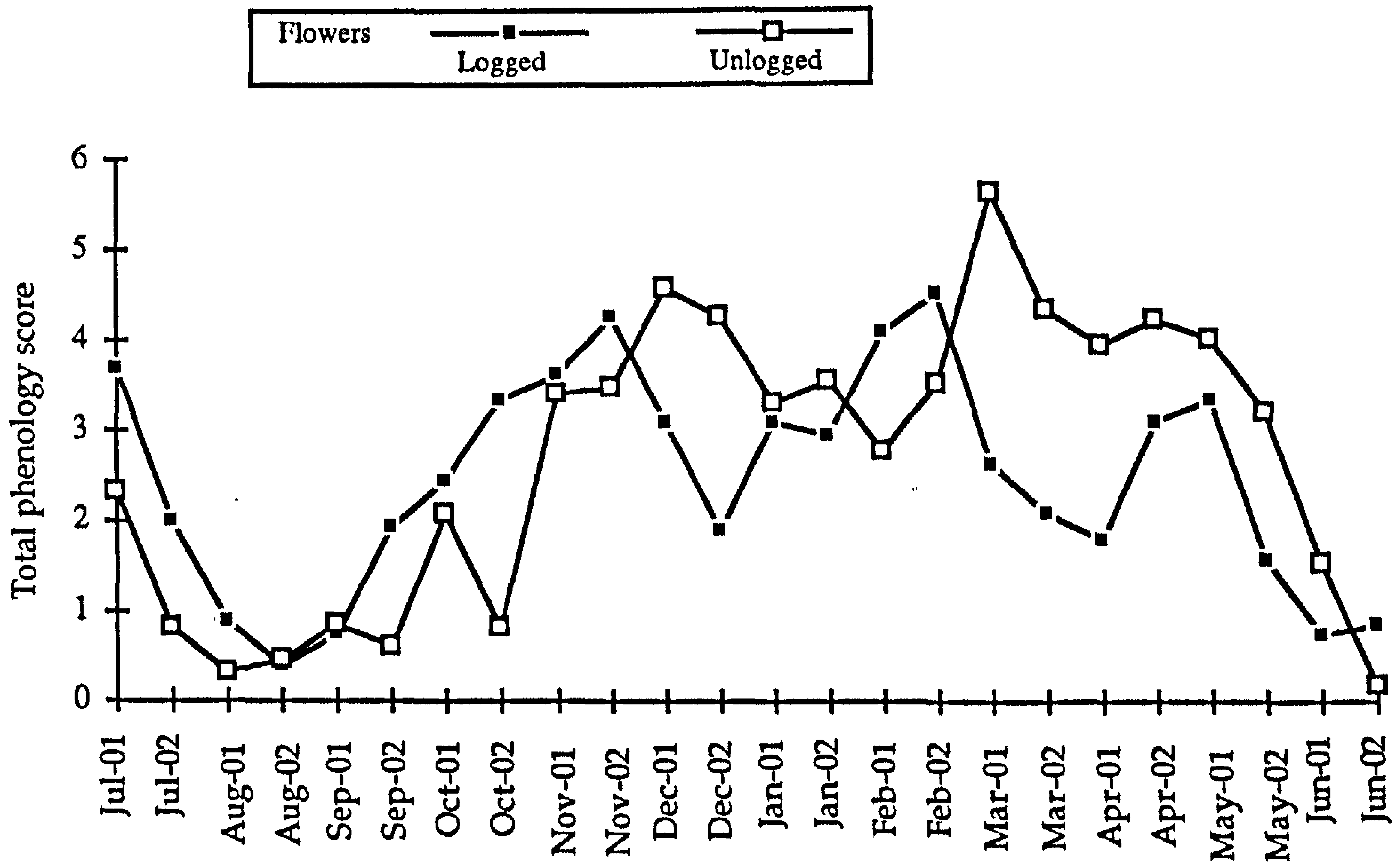


Figure 5.2.d. Flower production in logged and unlogged compartments (15 species combined)

Estimated availability of food items for the 15 tree species occurring within the two group ranges was calculated for each 2 week period .

Comparing the mean availability scores per plot for food categories for the 24 two week sample periods combined, differences are seen in the overall availability of leaves and fruit (Figure 5.3 and 5.4).

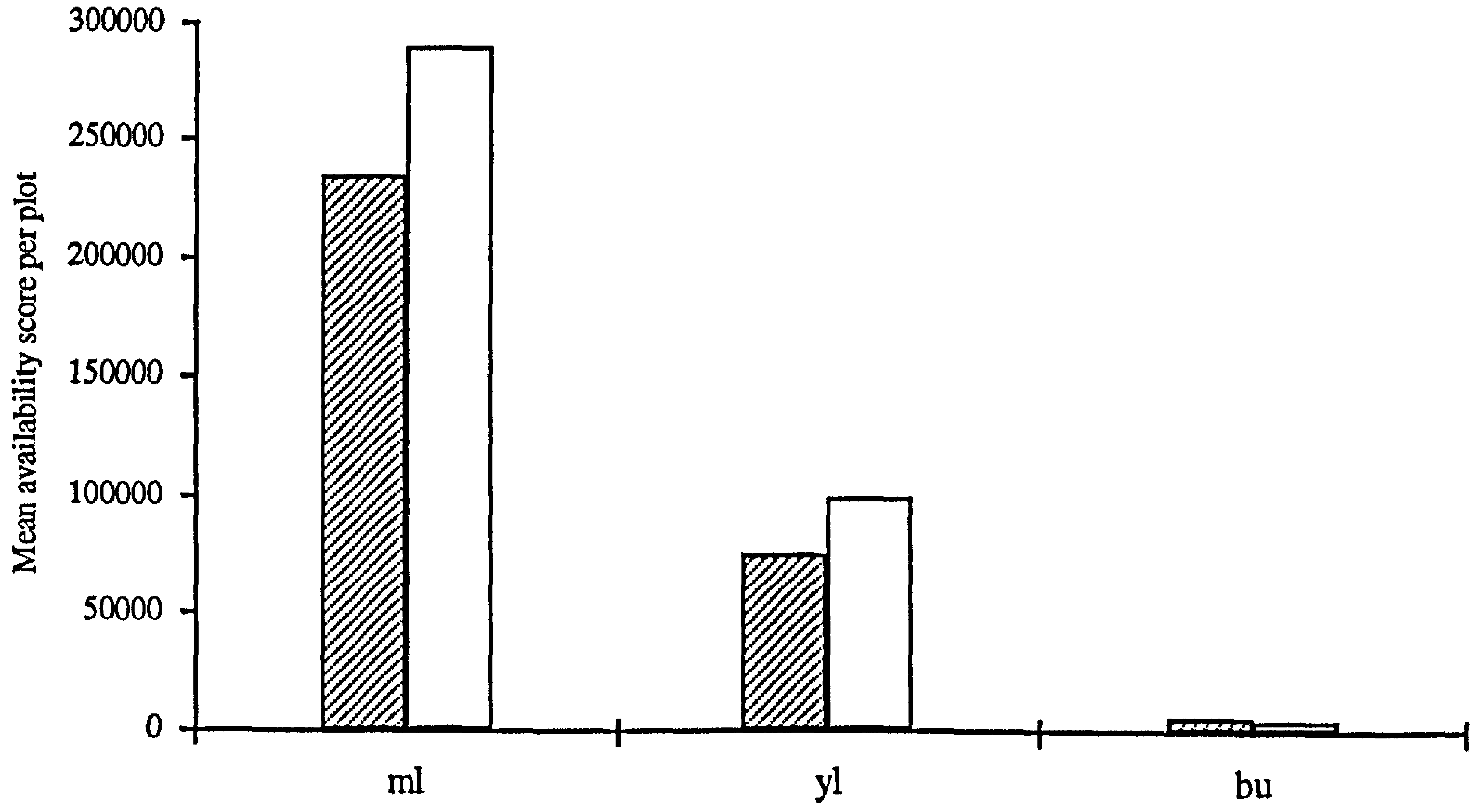


Figure 5.3. Mean availability of leaves and buds per plot calculated for 24 phenology sample periods: ▨ = N3 (logged) ☐ =N15(unlogged)

There is a much higher overall availability of mature leaves and young leaves per plot in N15 although there is no discernible difference for buds (Figure 5.3). The higher mean availability of vegetative plant parts in N15 reflects the continuous presence of mature leaf cover and the more regular flushing of young leaves throughout the year in N15.

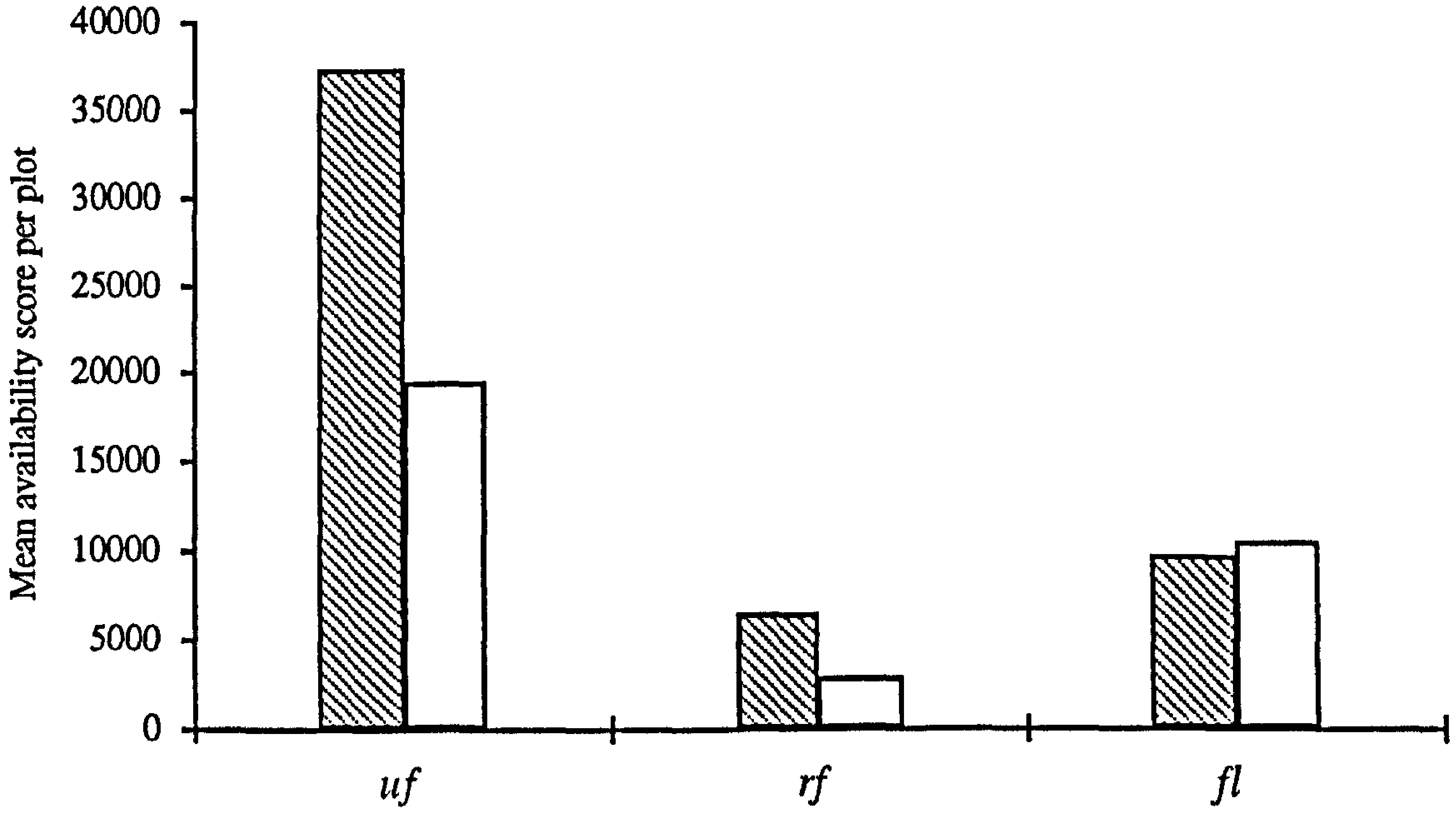


Figure 5.4. Mean availability of fruits and flowers per plot calculated for 24 phenology sample periods: ▨ = N3 (logged) ☐ =N15(unlogged)

The opposite is true for reproductive plant parts (i.e. fruits and flowers) which show a higher mean availability score per plot in N3 for the 24 week phenology period (Figure 5.4).

Seasonal Availability

Seasonal patterns in availability were then compared between compartment N3 (group N32 range) and N15 (group N151 range) graphically (Figures 5.5.a to 5.5.d) and by Wilcoxon Test (Table 5.3). Mature leaf and young leaf availability are significantly higher in N15 compared to N3 at most times of the year (Mature leaves: z=2.77, P<0.01; Young leaves: z=4.26, P<0.01;Table 5.3). This is due mainly to higher basal area of species such as *Cynometra alexandri, Celtis mildbraedii* and *Celtis zenkerii.* which produced young leaves throughout the year. N3 shows a more marked loss of mature leaves due to the high incidence of shedding in common species such as *Celtis durandii, Chrysophyllum albidum* and *Croton macrostachyus* (Figure 5.5.a). Bud availability does not show significant differences (z=1.714, P>0.05; Table 5.3), but appears to be have several peaks in production in N3 compared to N15 (Figure 5.5.b). Unripe fruit availability is significantly higher in N3 compared to N15 (z=3.371, P<0.01;Table 5.3), mainly due to the high basal area of species such as *Celtis durandii* and *Maesopsis eminii.* Ripe fruit availability is also significantly higher in N3 (z=3.257, P<0.01; Table 5.3). N3 unripe fruit availability is high initially, falling during the long dry season (Figure 5.5.c) while ripe fruit availability shows two well defined peaks in availability. N15 shows a more constant availability of ripe and unripe fruit but availability is much lower during most of the year. Flower availability shows no significant difference (z=0.629, P>0.05; Figure 5.5.d) but again appears to be more variable in N3 compared to N15.

Table 5.3. Wilcoxon z values and probabilities for tests between N3 and N15 food item availability for 15 shared sp.

N3/N15	z	P	Difference
Ripe fruit	3,257	<0,01	N3>N151
Unripe fruit	3,371	< 0,01	N3 > N151
Mature Leaves	2,77	< 0,01	N151 > N3
Young Leaves	4,26	< 0,01	N151 > N3
Buds	1,714	>0,05	ns
Flowers	0,629	>0,05	ns

Both N3 and N15 show a reduction in unripe fruit availability towards the end of the long dry season (Feb.-March) although there are still some ripe fruits available in N3 (Figure 5.5.c).

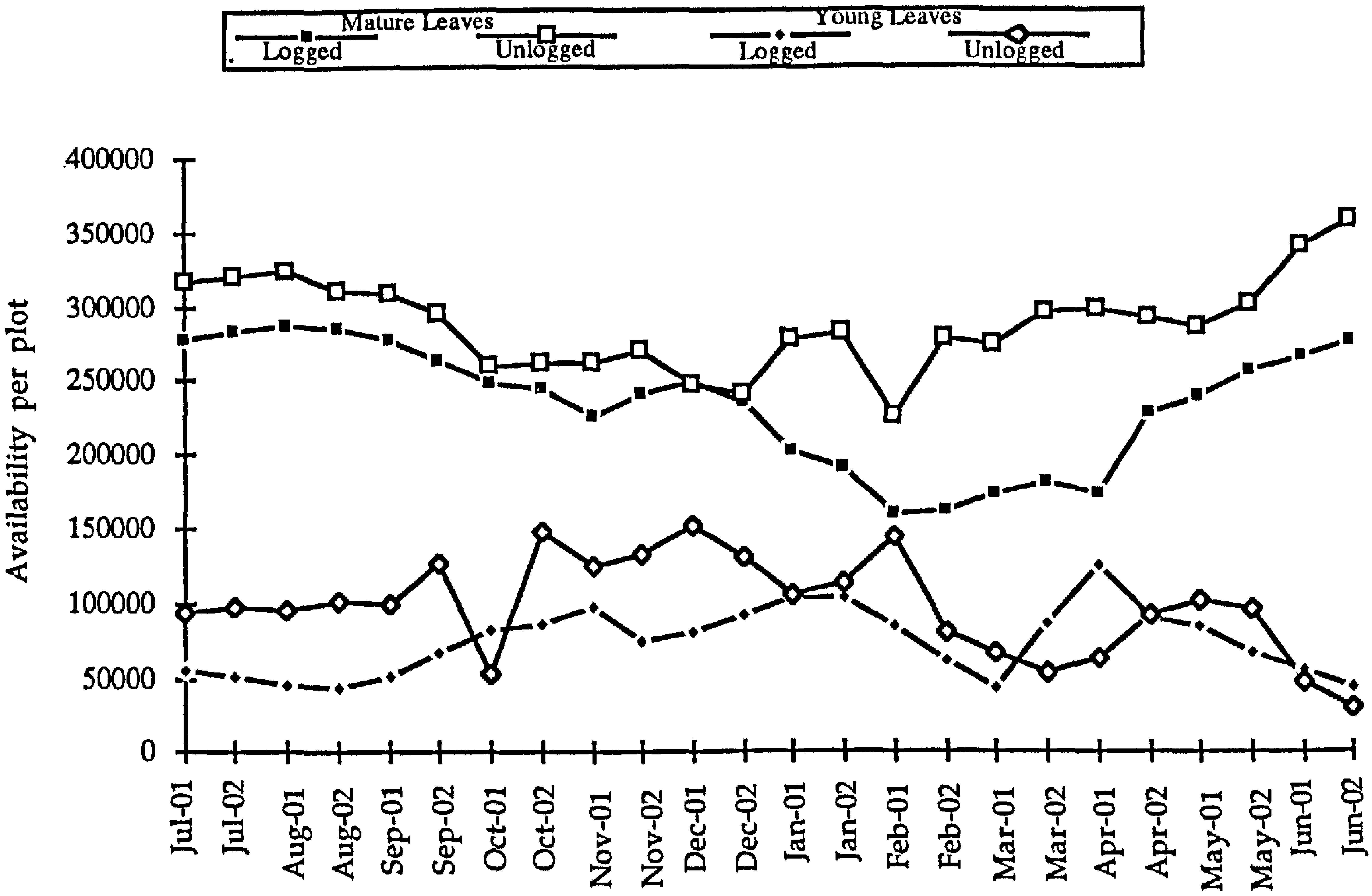


Figure 5.5.a. Seasonal availability of mature leaves and young leaves per 0.25 ha plot.

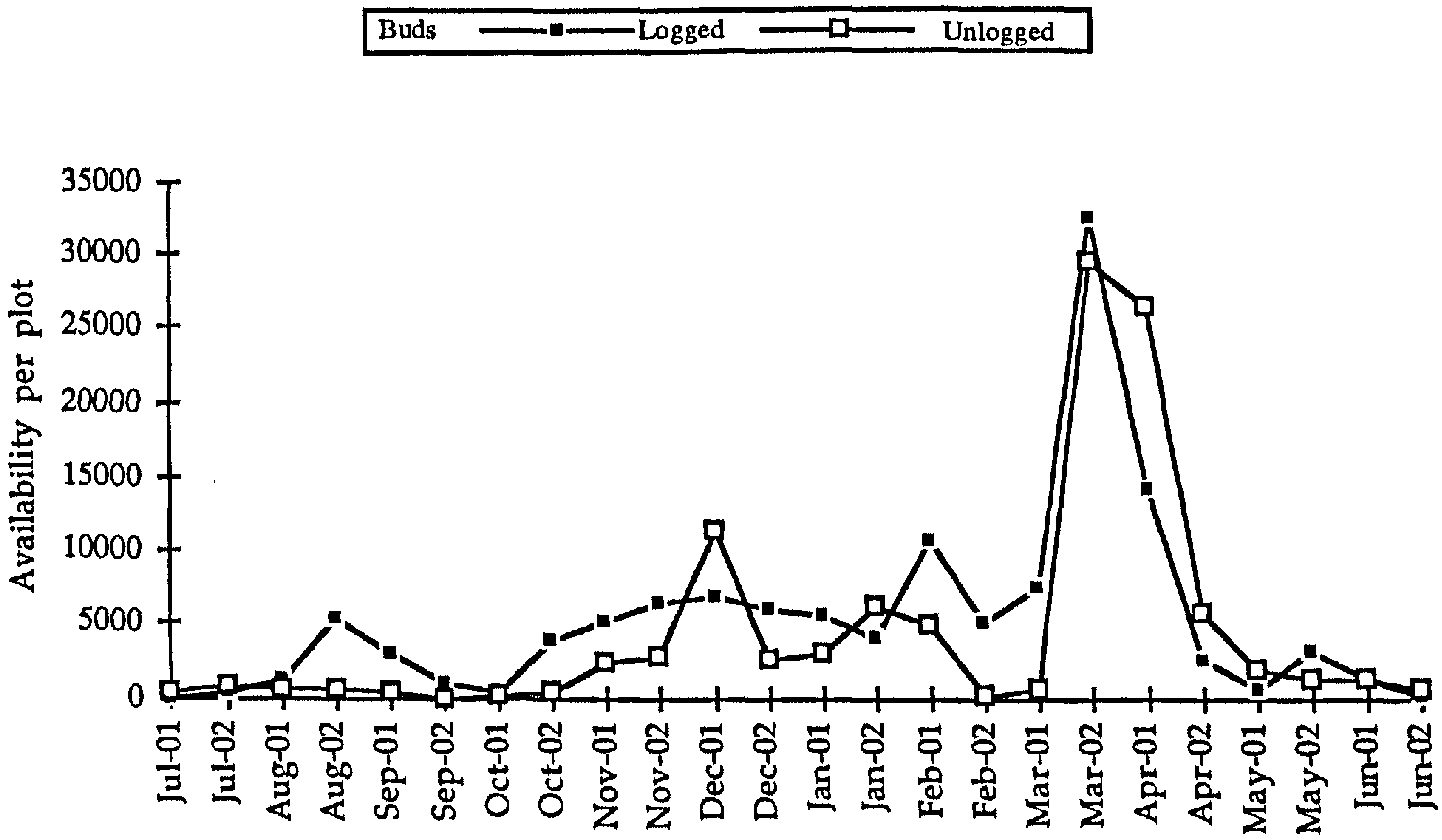


Figure 5.5.b. Seasonal availability of buds per 0.25 ha plot.

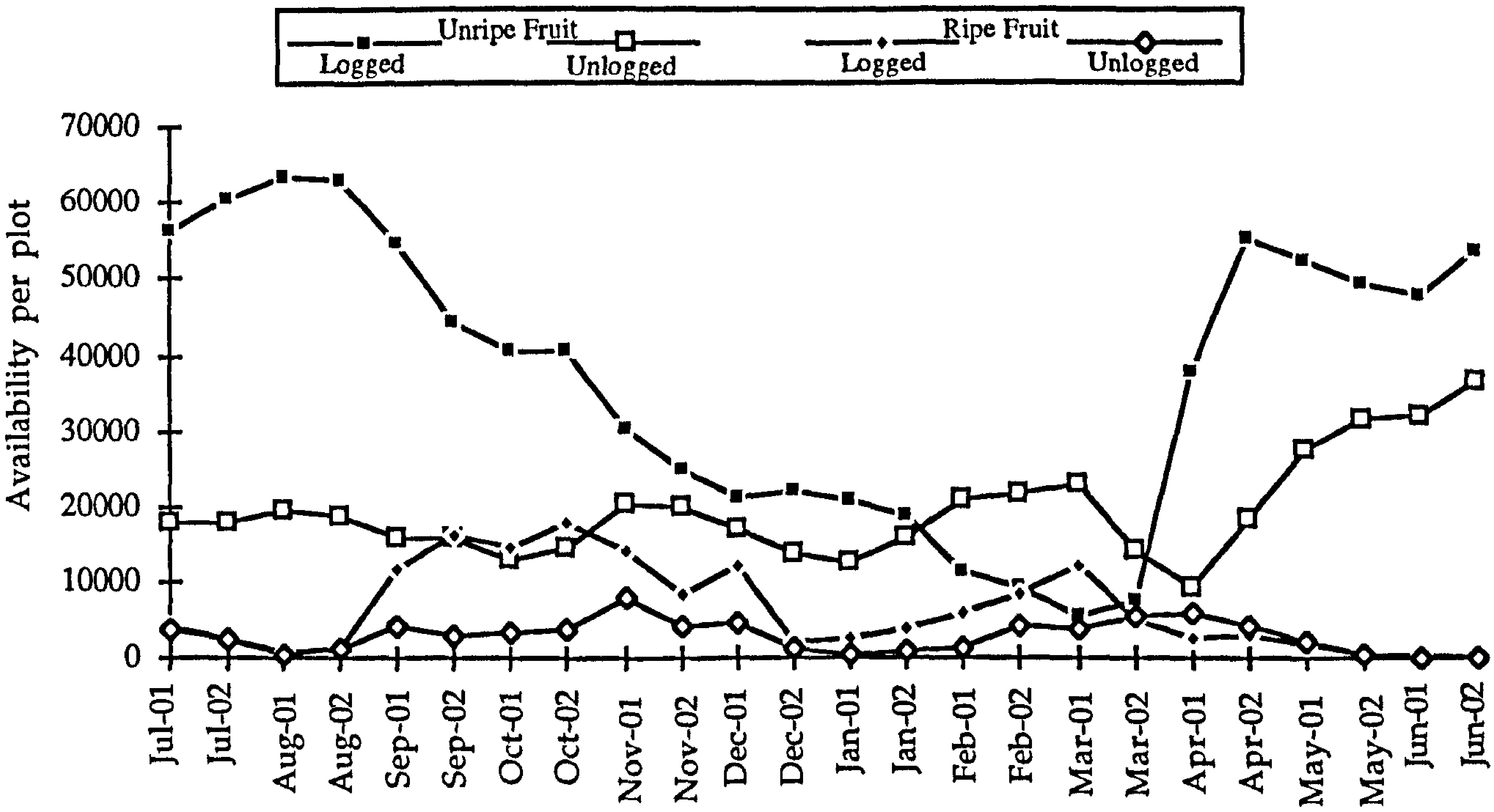


Figure 5.5.c. Seasonal availability of ripe and unripe fruit per 0.25 ha plot.

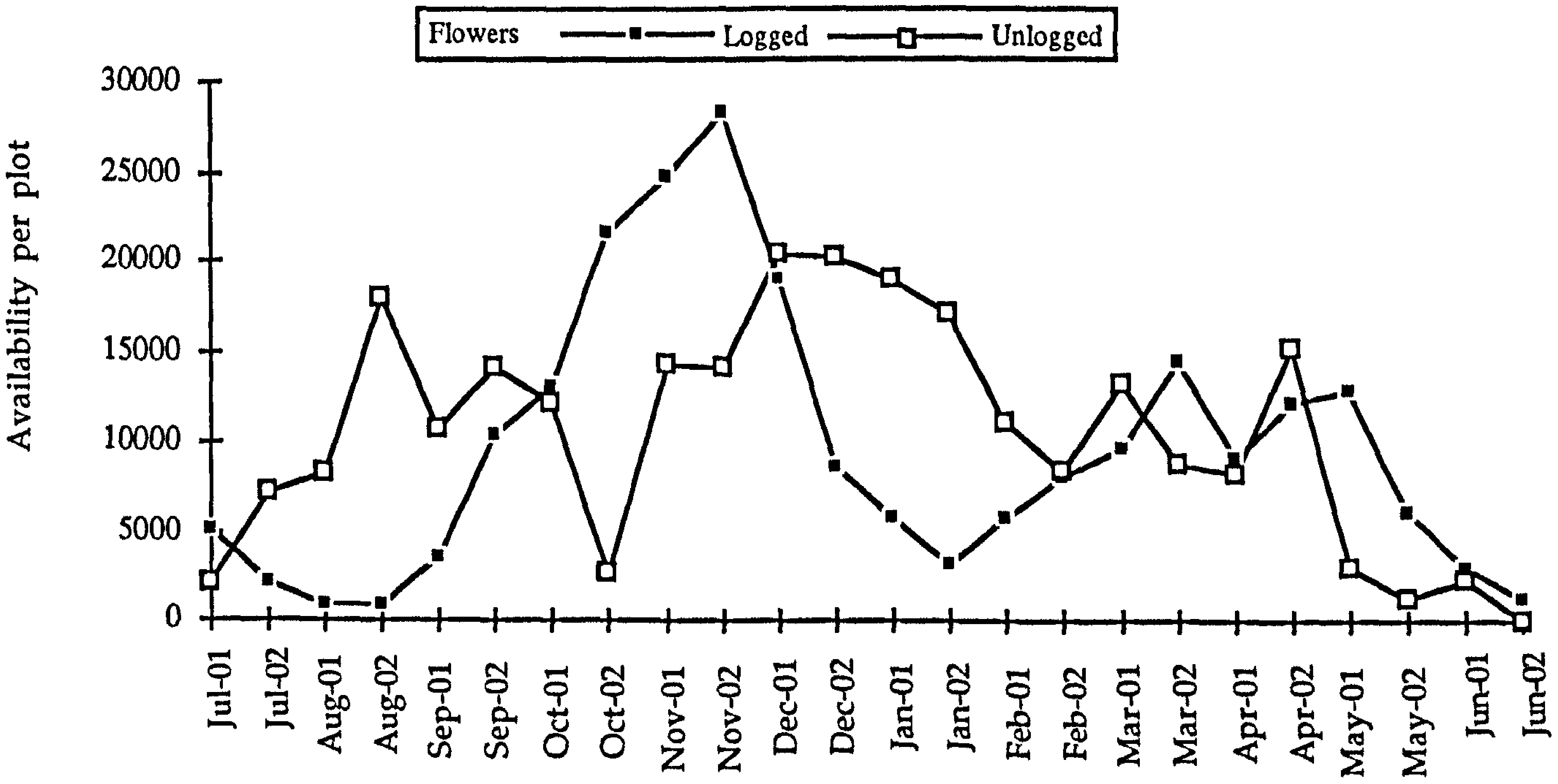


Figure 5.5.d. Seasonal availability of buds per 0.25 ha plot.

Comparison of the coefficients of variation for the same 24 two week availability scores show differences in the patterns of temporal availability for items in N3 and N15.

Table 5.4. Coefficients of variation for 24 two week phenology periods.

	ML	YL	BU	UF	RF	FL		All fruit	All items
N3 (logged)	17.95	30.67	129.8	51.22	86.44	78.79	-------	41.70	12.92
N15 (unlogged)	10.83	34.21	181.0	33.94	72.34	59.78	-------	26.65	6.05

A high Coefficient of Variation shows variability in availability across all sample periods. In other words, irrespective of the measure of availability, the variation in the measure over time is greater. In compartment N3, the coefficients of variation are higher for mature leaves, unripe fruit, ripe fruit and flowers. This shows that for these items, variation in availability is high across the year in logged forest (N3). By contrast, the coefficients of variation for buds and young leaves are higher in unlogged forest (N15) showing that there is higher variation in the production of these items throughout the year in N15.

5.4 DISCUSSION

Seasonal Phenology Patterns

Combining phenology scores from all tree species (both compartments) indicates very seasonal patterns of production for all plant items and these patterns of production appear to be closely related to rainfall. Mature leaves are present in all months with a reduction in the dry season (January-March) and peaks in young leaf production occur during the two wet seasons (September-November and March-May). The dry season reduction in mature leaves is due to leaf shedding, observed in a high proportion of deciduous trees present in Budongo (Synott 1985). The more noticeable peak in young leaves at the end of the long dry season (March-May: Figure 5.1.a) corresponds to a large scale leaf flushing as trees which had shed leaves in the dry season produce new leaves. The other peaks in young leaf production occur as mature leaves are slowly being lost and replaced throughout the year. Bud production occurs throughout the year but peaks strongly at the start of the rains (March-April). Previous studies have shown a similar reduction of mature leaf cover during dry periods and corresponding flushes of leaf buds and young leaves with the onset of seasonal rain (Lieberman and Lieberman 1986, Kinnaird 1992, Wright and Conejo 1990). Fruiting patterns overall are also distinctly seasonal, with bi-modal peaks in both unripe and ripe fruit production. Unripe fruit production increases in the dry seasons and ripe fruit production commences with the onset of the rains. Flower production shows bi-modal peaks occurring at the beginning and at the end of the dry season. Chapman et al (1994) documented seasonal patterns in plant part production in higher altitude at Kibale Forest, Uganda where the climate is similarly seasonal. White (1994c) also reported an increase in fruit production with the onset of rain while Tutin and Fernandez (1993), working at the same site, found mean minimum temperature during the dry season months to be important in determining fruit production patterns in the following seasons. They concluded that this influence was likely to operate through the timing of flower production in the dry season. Strong seasonality, especially in a semi-deciduous forest such as Budongo is well documented (Lieberman and Lieberman 1986, Longman and Jenik 1974, van Schaik et al 1993) and tree species from both N3 and N15 exhibit these seasonal patterns.

Seasonal Production Of Blue Monkey Food

Comparing the production scores for different items between N3 and N15, there are no significant differences. However, there do appear to be differences in the timing of peaks in unripe fruit and young leaf production between the two areas. N3 (logged forest) shows higher unripe fruit and young leaf production compared to N15 (unlogged forest). Differences in the production patetrns may be due to the heterogeneity of the canopy in logged forest and the different reproductive strategies of colonising and mature forest species (Rodman 1978). Fimbel (1994) found leaf production to be more variable throughout the year in secondary forest while fruit production was more even in secondary forest compared to old forest. Burghouts et al. (1994) documented greater seasonality in leaf fall in old forest while logged forest showed a more even distribution of leaf fall throughout the study period. The seasonal patterns of fruit production in N3 show a high production of unripe fruit in the early part of the study, declining through the long dry season and subsequently increasing again. The pattern in N15 shows low initial production but a higher level of production in the dry season. This increase in production is probably due to species such as *Entandrophragma sp.* and *Alstonia boonei* producing wind dispersed, non-fleshy fruits, and therefore does not indicate an increase in fleshy fruit production. An increase in production of unripe and ripe fruit in logged forest may be caused by more individuals of a smaller size being present for a given tree species in logged forest. For tree species associated with colonising forest, canopy heterogeneity and associated higher light levels may enhance fruit production (Foster 1980, Rodman 1978). Treefall gaps may be more common in logged forest and may create heterogeneity in climatic conditions which in turn influence patterns of fruit and leaf production (Levey 1990).

Seasonal Food Availability: Logged vs. Unlogged Forest

Food availability differences occur due to differences in timing of production as described above and also due to differences in the mean basal area per plot for certain tree species. Unlogged forest shows a significantly higher availability of mature leaves and young leaves while logged forest shows a significantly higher availability of ripe and unripe fruit. Both N3 and N15 show reduction in mature leaf cover during the dry season but this reduction is less marked in N15 (logged forest). This reflects differences in the composition of the total basal area between the two areas. N15 has a high basal area of mature forest species such as *Cynometra alexandri, Entandrophragma spp* . and *Celtis mildbraedii* as well as several common understorey tree species (see Chapter 5). In addition to being large and potentially slow-growing individuals, most of these species do not shed their leaves in the dry season and produce less fruit throughout the year. The fruits which are produced are largely arillate or have very hard seeds, are dispersed by wind or explosive mechanisms and are apparently not preferred foods for primates such as blue monkeys (see Chapter 7). The species composition of N3, by contrast, reflects a high basal area of 'colonising' species (eg. *Maesopsis eminii, Celtis durandii, Ficus spp.* and *Croton macrostachyus*). The individuals of these tree species are probably faster growing, fruit more regularly throughout the year and mostly produce fleshy fruits for zoochorous dispersal.

Fruit availability in N3 occurs in two well defined peaks corresponding with the wetter periods and unripe fruit in particular is available for a longer period throughout the year in N3 compared to N15. Fimbel (1994) also documents fruit being generally available during one annual cycle in young re-growth forest while in old forest, fruit production was much more seasonal. Flower and bud availability are similar in N3 and N15 except for a slightly higher more concentrated peak in flower availability in logged forest. Comparing coefficients of variation (a measure of the annual variation in a bi-weekly value) some differences are seen between logged and unlogged forest. Mature leaf production shows less annual variation in unlogged forest compared to logged forest as does ripe fruit, unripe fruit and flower production. Young leaf and leaf bud production shows more annual variation in unlogged forest compared to logged forest. As a consequence, fruit availability in unlogged forest is lower and is less variable. Fruit availability in logged forest is at higher level throughout the year and shows more variation throughout the year. Comparing the phenological patterns observed in the different forest types studied here with those described previously, there is some evidence that general trends in phenological production may be detectable between disturbed and undisturbed forest (Burghouts et al. 1992, 1994, Johns 1991b, Rodman 1978, van Schaik et al 1993). Van Schaik (1986) recorded a higher level of variation in timing of leaf production in 'young' forest in Sumatra due to a higher proportion of trees shedding their leaves. In contrast to this study fruit production was less variable in time in young forest compared to mature forest.

Discussing synchrony in leaf production, van Schaik et al (1993) suggested that predation of leaves and competition may result in a much more asynchronous leaf production. Nascimento and Proctor (1994) described the effect of a defoliating caterpillar on leaf cover in an Amazonian monodominant forest and concluded that such predation may be important in determining leaf production patterns. There were several occasions where heavy infestations of caterpillars were observed in *Cynometra*- mixed canopy in unlogged forest (pers. obs). Mature forest species in *Cynometra* monodominant forest may also experience such predator effects and these in turn may be important in explaining the difference in observed phenological patterns - higher levels of predation may lead to more variation in production of young leaves and leaf buds, but a more constant cover of mature leaves.

Inter specific competition for dispersers and pollinators may also play a role in determining the different patterns of fruit and flower production observed. There may be more competition for pollinators/dispersers in logged forest and as a result, the production of reproductive plant parts is more variable throughout the year (sensu.Van Schaik et al 1993). These phenological differences translate into a higher availability and more variable production of fruit and flowers in logged forest with a lower but more constant production of young leaves and buds. Unlogged forest by contrast shows a high but variable availability of young leaves and leaf buds with a low but more constant availability of fruits and flowers.

Ficus spp and Dry season Food Shortages

It should also be noted that although the 15 species compared do not represent the whole diet spectrum for all 4 groups, they do include more than 60% of the top 20 food items in all groups (see Chapter 7). As the assemblage of 15 tree species compared in the two areas does not include several species of *Ficus* common in compartment N3, it is important to observe that the estimate of fruit availability in N3 is probably a minimum one. It is clear that fruit availability in N3 would be much higher if the production of fruit by *Ficus sur, Ficus exasperata* and other *Ficus spp.* was included (unpubl. data). It is also of interest to note that the majority of individuals of *Ficus* in N3 produced fruit and leaf buds during the dry season (Figure 5.6) which would increase the availability of fruit during this period of shortage if included in the estimate.

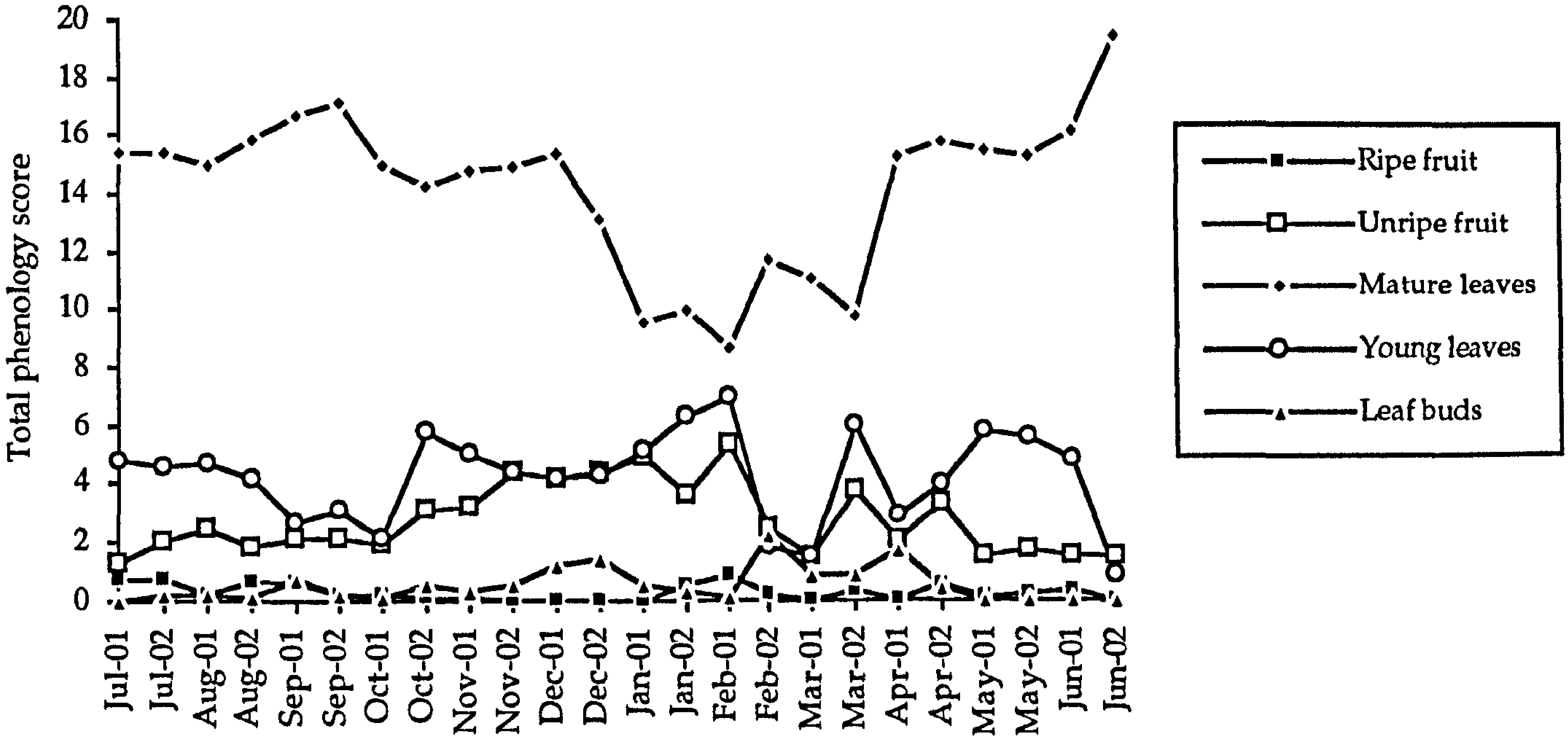


Figure 5.6. Seasonal patterns of plant part production for 38 individuals of five *Ficus* spp. in logged forest.

The remaining proportion of the diet for unlogged forest groups is made up of fairly rare species, climbers and strangling figs (*Ficus lingua, Alaphia landolphioides, Ficus natalensis, Teclea noblis, Antiaris toxicaria*) therefore the addition of these items to the production/availability estimates would be unlikely to result in a significant increase in the estimate. These rare species are obviously important as dietary items during the period of food shortage (December-March), but they are present in much lower quantities in the habitat and as a result groups in logged forest experience a lower availability of food.

Conclusions

i) Overall phenological patterns of important blue monkey food trees are distinctly seasonal and appear to be closely determined by rainfall patterns

ii) Within the annual cycle, there are some differences in production between logged and unlogged forest with higher production of unripe fruit and young leaves in logged forest during the wet periods.

iii) These differences, combined with the different species composition and relative abundance (see Chapter 4), result in different estimates of overall food availability. Logged forest has a higher and more variable (within year) availability of fruit compared to unlogged forest where fruit availability is lower and less varaible. Unlogged forest shows a higher availability of leaves with mature leaves showing less within year variation but young leaves showing more within year variation.

iv) Dry season food shortages which are likely to occur in both logged and unlogged forest may be less severe in logged forest due to the presence and fruiting patterns of several *Ficus* species which were not present in unlogged forest.

CHAPTER 6

POPULATION DENSITY AND DEMOGRAPHY

6.1 INTRODUCTION

As discussed in Chapter 2 there is considerable variation in the population density (individuals/km^2) of blue monkeys at various sites where they have been previously studied. The range of densities probably reflects variation in carrying capacities between different habitats (Butynski 1990). Factors that may be important in determining carrying capacity include: historical factors, food availability, inter-specific competition for food, and mortality rate (Butynski 1990, Oates et al 1990, Struhsaker 1978). As well as varying between forest type, carrying capacity may also vary within forest types as a response to changes in forest structure subsequent to logging or other disturbance (Lawes 1992, Skorupa 1986).

Changes in the population density of primate species may have consequences for group size, structure and demography (Butynski 1990, Cords and Rowell 1986) , but the effects of logging on these is little known (Johns 1981). In undisturbed forest, group fission has been recorded in response to increasing population density (Cords and Rowell 1986, Lwanga 1987). Group structure in blue monkeys is generally found to be matrilineal with one resident male per group (Cords 1988) although variations in mating systems have been recorded in different habitats and in different seasons (Cords et al. 1986, Henzi 1988). Births have been observed to occur throughout the year but with a seasonal peak in several studies (Gevaerts 1992, Rowell and Richards 1979). Owing to the relatively slow reproductive rate of primates, difficulties exist in gathering the long term data necessary to document demographic changes and determine their causes. Johns (1981) documented an increase in the infant mortality rates of *Hylobates lar* and *Presbytis melalophos* immediately after logging, but the direct causes of this increase were unclear. Butynski (1990), studying two populations of *C.mitis* at very different densities, discussed differences in male-male competition, birth rates and territoriality in the two study sites. Obviously factors such as mortality rates and reproductive output play an important role in determining the survival or extinction of primate populations following logging.

6.2 METHODS

Population density estimates of all primate species in logged (8 compartments) and unlogged (2 compartments) areas of Budongo Forest were made by Dr. A.Plumptre. These estimates were arrived at by carrying out censuses and performing Distance analysis (see Plumptre and Reynolds 1994 for details). These density estimates for all logged and all unlogged compartments are shown below, together with densities for the two sites for this study (Compartment N3 and Compartment N15). For these two compartments, density estimates for blue monkeys, redtail and black and white colobus were used to calculate the ratio of blue monkeys to other species in the areas used by the study groups.

For the four study groups, counts were obtained during dawn to dusk follows and averaged to give a group estimate for each month. Locations and group counts of other blue monkey groups in the study sites were obtained during dawn to dusk follows and opportunistic observations of other groups in the two compartments. Locations were recorded and plotted in relation to the estimated ranges of the four study groups. For non study group counts, only those which were thought to be reasonably complete are included and, because of the difficulty involved in counting un-habituated groups, these counts are likely to represent minimum estimates. Locations of other groups (all species) moving in areas adjacent to or overlapping with study group home ranges were recorded throughout the study period and mapped to give some indication of a) the number of other groups adjacent to the study groups and b) the degree of overlap in range between study groups and adjacent groups.

During scan sampling, association with redtail groups was recorded and the proportion of all scans spent in association was calculated. Despite the design of sampling procedures to give random samples of age-sex classes in groups, some age-sex classes were sampled more than would be expected by chance. Data were tested to compare the observed and expected frequency of scans for each age-sex class (Chi Squared test). Expected scores were calculated using proportions of each age-sex class from group counts. Correction factors were applied to data where age-sex classes had been sampled more frequently than was expected by random sampling. The distribution of completed scans throughout the diurnal sampling period was also plotted to show the distribution of completed scans throughout the day for each group.

6.3 RESULTS

Primate Densities

Population densities of three species - *Cercopithecus mitis stuhlmanni* , *C. ascanius schmidtii* and *Colobus guereza occidentalis* - were higher in all logged compartments as compared to all unlogged compartments (Table 6.1: data from Plumptre et al.1994). Differences for the other two species (*Papio anubis* and *Pan troglodytes*) were not significant but estimates were higher in unlogged forest. When only compartments N3 and N15 are considered, differences are significant for four species (data for one species not sufficient to test for differences). Comparing blue monkey density in compartments N3 and N15, there were almost twice as many individual blue monkeys per km^2 in the logged compartment. This difference was less marked as compared to the difference in density between all logged compartments versus all unlogged compartments. The very low blue monkey density recorded in the second unlogged compartment considerably reduced the estimate for all unlogged forest compartments (A.Plumptre pers comm.).

Table 6.1. Densities of five primate species in Compartments N3 (logged) and N15 (unlogged)[†](From Plumptre et al. 1994, Plumptre unpubl. data)

Species	Compartment N15 (unlogged) no/km^2	Compartment N3 (logged)no/km^2	T-test[§]
Cercopithecus mitis	31.2	57.5	**
(Blue monkey)	(15.6)	(58.2)	***
Cercopithecus ascanius	12.5	38.75	**
(Redtail monkey)	(8.3)	(46.4)	***
Colobus guereza	26.0	52.3	*
(Black and White colobus)	(27.0)	(44.2)	****
Pan troglodytes	0.9	1.25	*
(Chimpanzee)	(1.4)	(0.8)	ns
Papio anubis	n/a	n/a	n/a
(Olive baboon)	(14.0)	(11.0)	ns

[§] T-tests for differences: n/a = data not savailable ns = $P>0.05$, * = $P<0.05$, ** = $P<0.01$, *** = $p<0.001$.

[†] Figures in brackets show densities calculated from all logged compartments and all unlogged compartments

The ratio of *C.mitis* : *C.ascanius* : *Colobus guereza* was 1 : 0.4 : 0.83 in compartment N15 and 1 : 0.67: 0.91 in compartment N3. Therefore there are not only more blue monkeys per unit area but also more individuals of the other two species per blue monkey in the logged compartment.

Plotting opportunistic sightings of conspecific non study groups in relation to the ranges of the four study groups gives some indication of degree of overlap between study groups and conspecific neighbouring groups. Each location point represents a single sighting of a group for each species. Figures 6.1.a to 6.2.b show the outlined ranges of the four study groups and individual sightings of conspecific and allospecific groups in the vicinity (each symbol represents a sighting of another group). All of these sightings were made opportunistically during dawn to dusk follows but since similar lengths of time were spent following each group (see below), they give an approximate idea of the occurrence of non-study groups of blue monkeys and groups of other species.

○ Blue monkey □ B+W Colobus △ Redtails

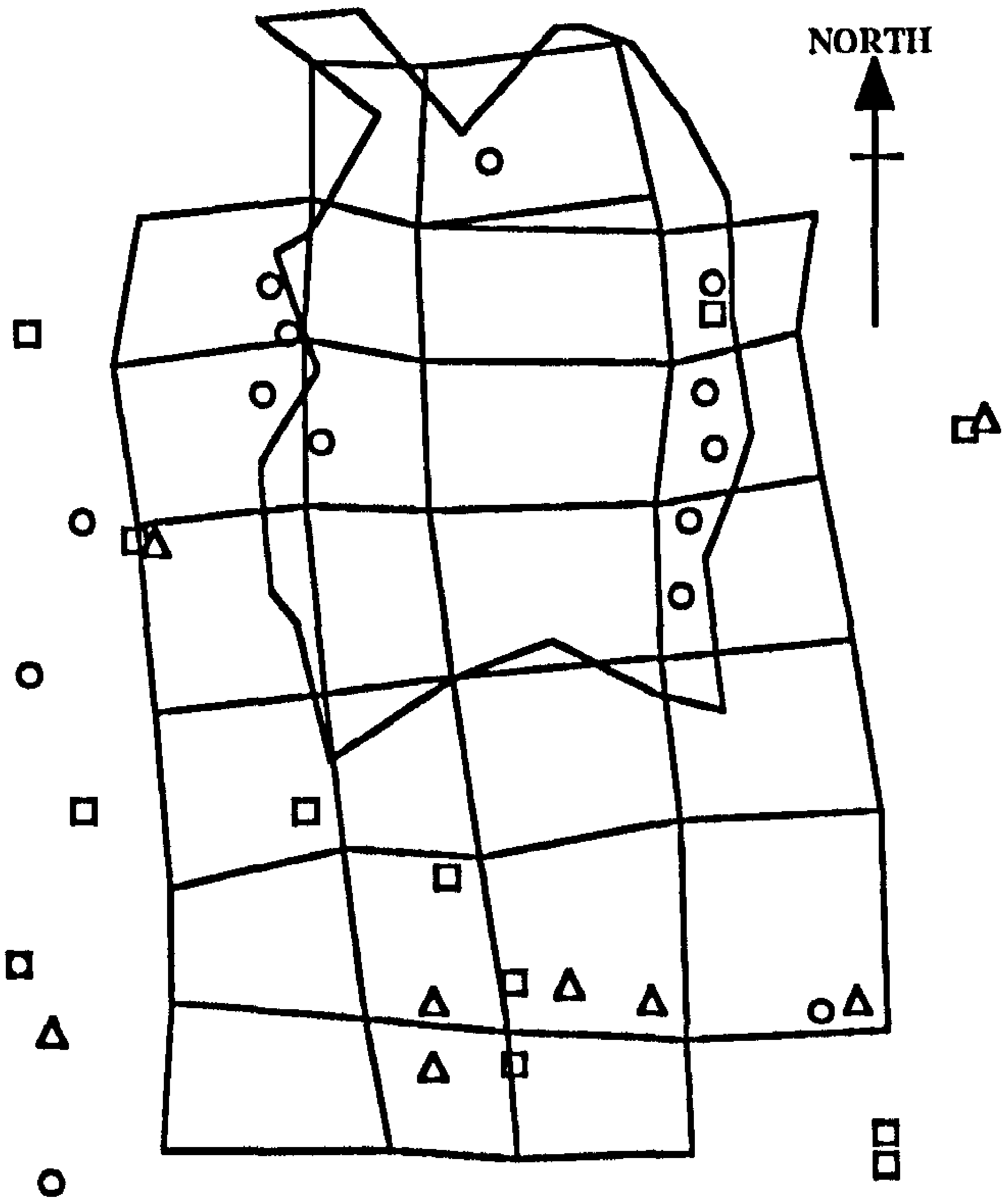


Figure 6.1.a. Location of conspecific and allospecific groups in relation to N31 Range.

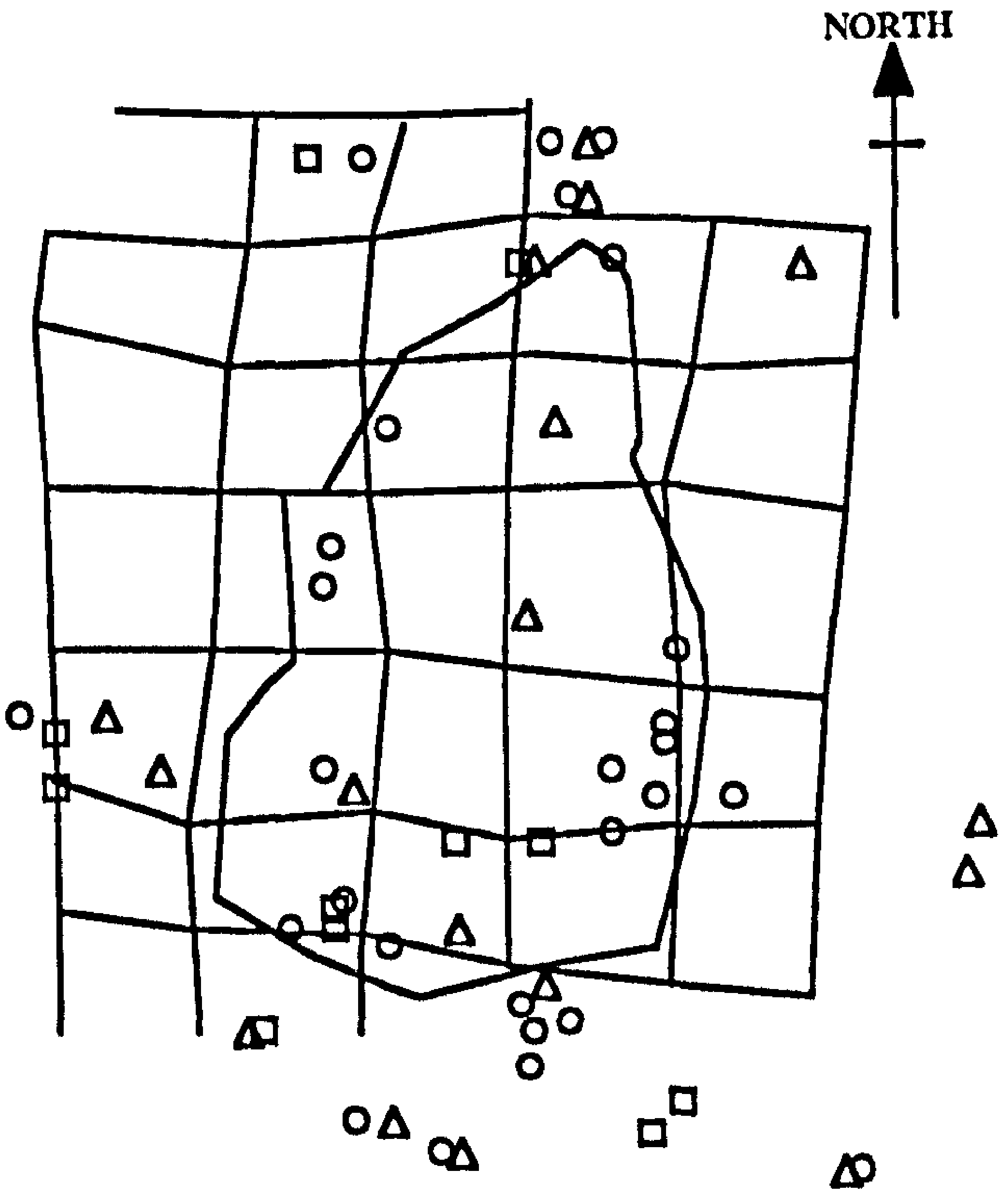


Figure 6.1.b. Location of conspecific and allospecific groups in relation to N32 Range.

All four groups show some degree of overlap with other blue monkey groups although sightings of other groups of blue monkeys were on the periphery of the estimated range for all groups. There were fewer sightings of redtail and colobus groups in unlogged forest, reflecting the lower densities of these two species, and suggesting that the level of inter specific competition may be lower in Compartment N15.

○ Blue monkey □ B+W Colobus Δ Redtails

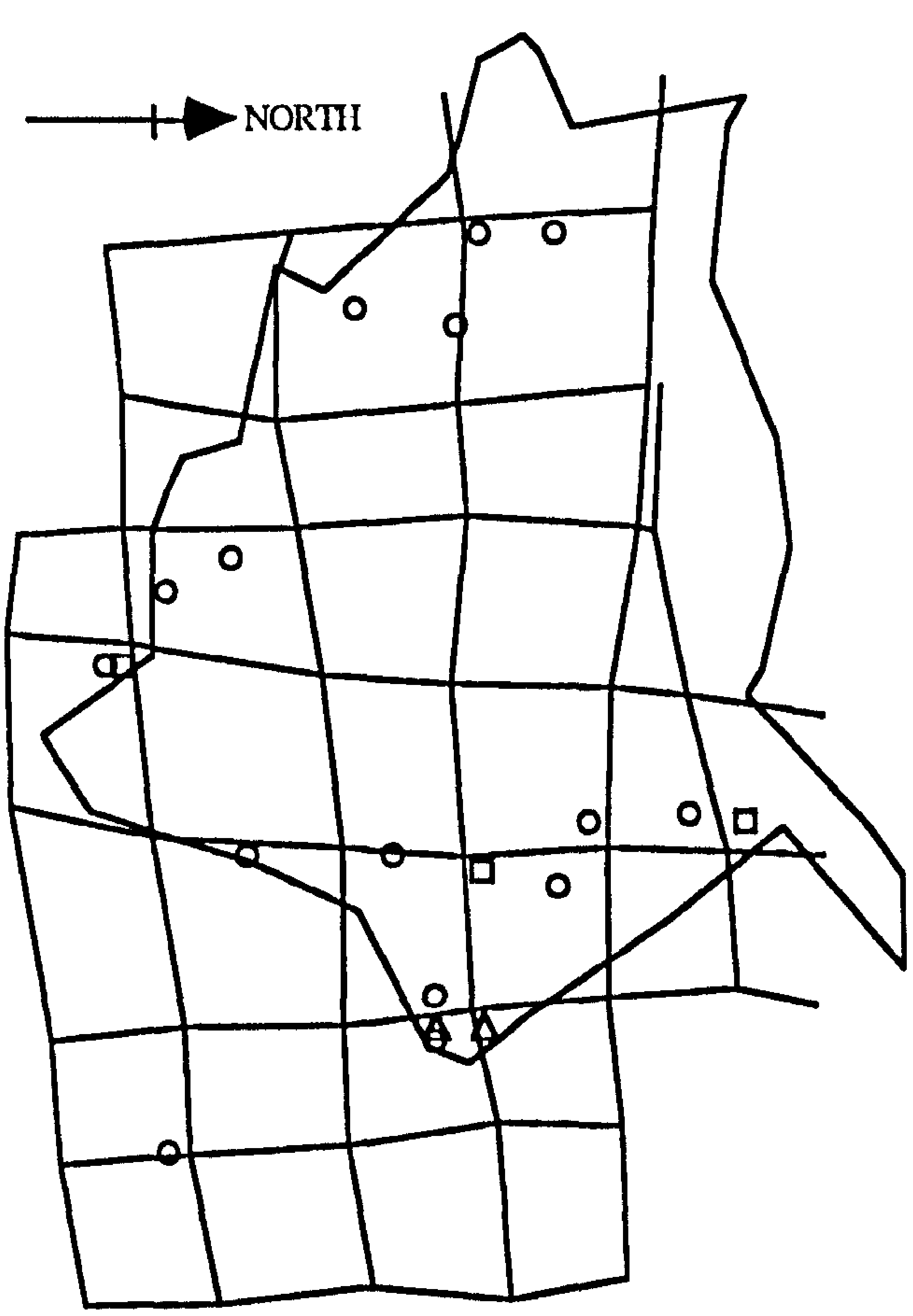


Figure 6.2.a. Location of conspecific and allospecific groups in relation to N151 Range.

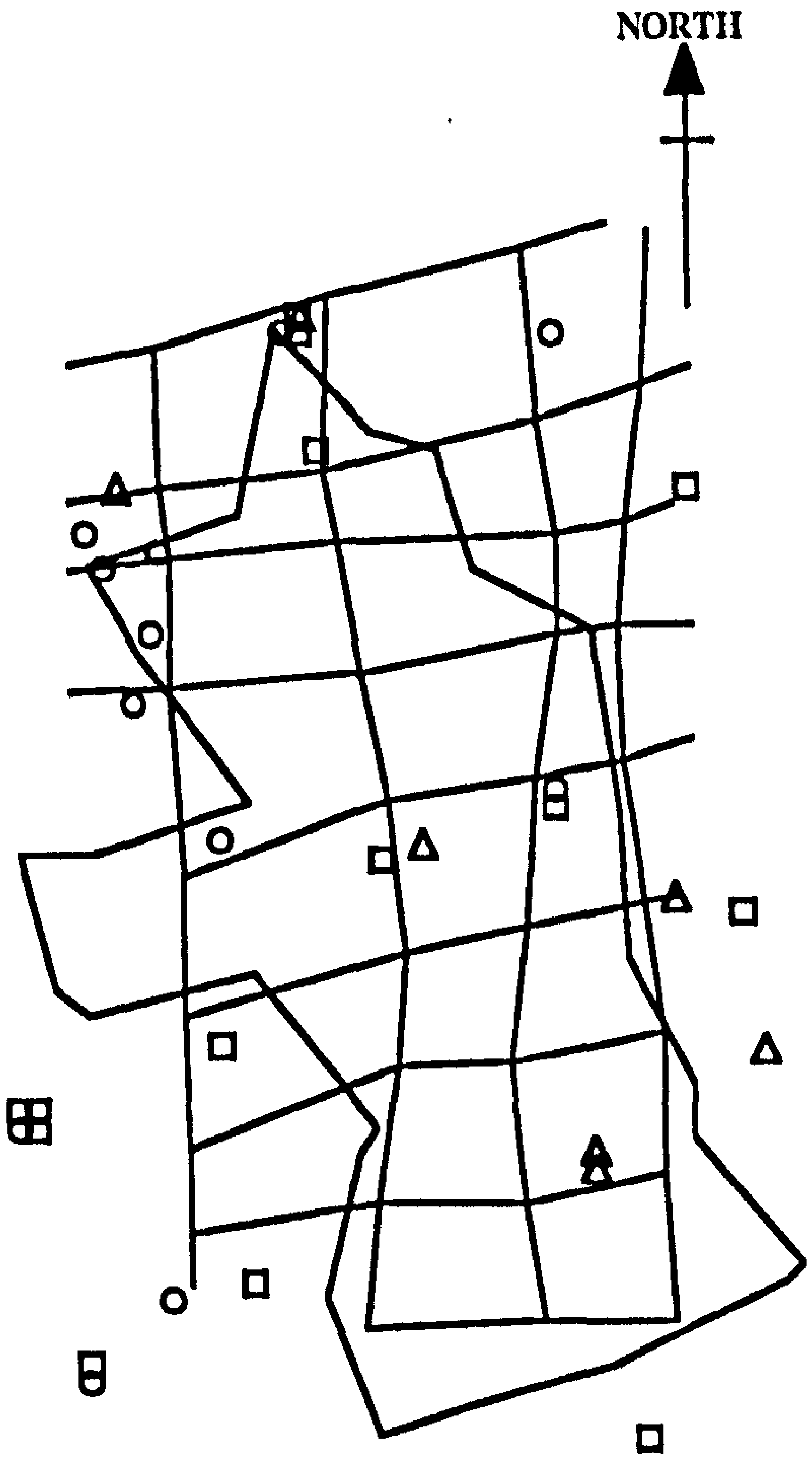


Figure 6.2.b. Location of conspecific and allospecific groups in relation to N152 Range.

Mixed Species Association

Group N32 spent the highest proportion of all scans in association with redtail groups, followed by N151, N152 and N31 (Table 6.2). There was no difference of proportion of time spent in association between logged and unlogged forest. However, given the different relative densities of the two species in the two compartments the degree of association must be expressed relative to the number of redtail groups per group of blue monkeys in the compartment. This gives a crude index (I_{RT} = index of 'redtail association') of time spent in association relative to the ratio of redtail:blue monkey groups (N3: 0.67:1; N15: 0.4:1). This index is based on the proportion of scans scored for association with *C.ascanius* divided by the ratio of redtail groups : one blue monkey group. Given the much lower ratio of redtail groups:blue monkey groups in the unlogged compartment, this index is higher for groups in N15 compared to N3. This suggests that both groups in unlogged forest are spending more time in association with redtails relative to their density.

Table 6.2. Proportion of all scans recorded in association with redtail monkeys for the four study groups.

Group	Proportion of all scans recorded in association	I_{RT}
N31	0.13	0.19
N32	0.23	0.34
N151	0.18	0.46
N152	0.14	0.36

Group Composition

Accurate group counts were made during the latter stages of habituation and throughout the 12 month study period and are summarised by month in Table 6.3. The four study groups do not differ greatly in size or composition although both groups in the unlogged compartment appear to have higher numbers of infants. As with most other previous studies, all groups had one resident male, although immature males were present in most groups at certain times.

Demographic changes were recorded and are indicated in Table 6.3. In some cases group counts may have been incomplete hence apparent changes (e.g. in the number of females in a group). Births appear to be spaced throughout the year but with a peak around January/February (dry season). There were no observed mortalities except one infant which was killed in September 1993 (see Fairgrieve (1995) for details), but some inferred emigrations may have been unobserved mortalities.

Table 6.3. Monthly Group Composition from May 1993 to July 1994.

Month	Group Counts : Ad.m Ad.f S.Ad Juv Inf							
	N31		N32		N151		N152	
May	1 3 3 3 0	10	1 4 3 3 0	11	1 3 4 3 1	12	1 4 2 3 2	12
June	1 3 3 $2_?$ 0	9	1 3 3 3 0	10	1 4_t 4_i 4_t 0	13	1 4 3_t 2 2	12
July	1 3 3 2 0	9	1 4 3 3 0	11	1 4 4_e 3 0	12	1 4 2_e 2 $1_?$	10
Aug	1 4_t 3 2 0	9	1_e 4 3 $2_?$ 0	10	1 4 4 3 0	12	1 4 2 2 1	10
Sept	1 4 3 2 0	10	1_r 4 3 3 1_b	12	1 4 4 3 0	12	1 4 2 2 2_b	11
Oct†	1 4 4_i 2 0	11	1 4 3 3 0_d	11	1 4 4 3 0	12	1 4 3_t 2_t 1	11
Nov	1 4 3_e 2 0	10	1 4 3 3 1_b	12	1 4 4 3 0	12	1 4 3 2 1	11
Dec	no count made	--	1 4 3 3 1	12	1 4 3_e 3 1_b	12	no count made	--
Jan	1 4 3 2 2_b	12	1 4 3 3 1	12	1 4 3 3 1	12	1 4 3 2 1	11
Feb	1 4 3 2 2	12	1 4 3 3 1	12	1 5_t 2 3 3_b	14	1 4 3 2 1	11
Mar	1 4 3 2 2	12	1 4 3 3 1	12	1 5 2 3 3	14	1 4 3 2 2_b	12
Apr	1 4 3 3_t 1	12	1 4 3 3 1	12	1 5 3 3 4_b	15	1 4 3 2 2	12
May	1 4 3 3 1	12	1 4 3 3 1	12	1 5 3 4_t 3	16	1 4 3 2 2	12
June	1 4 3 3 1	12	1 4 3 3 1	12	1 5 2_e 4 3	15	1 4 3 3 2	12
MEDIAN	1 4 3 2 0	10	1 4 3 3 1	12	1 4 3 3 1	12	1 4 3 2 1	11

Codes: **Adm** = Adult male; **Adf** = Adult female; **SAd** = Sub-adult; **Juv** = Juvenile; **Inf** = Infant
b = Births; **d** = Deaths ; **r** = male replacement; **i** = immigration; **e** = emigration; **t** = transfer from one age-sex class to the next; **?** = unknown change in group (this may be due to individuals being missed during counts) .
† The male replacement in Group N32 which occurred in September 1993 was followed by the killing of an infant by the male (see Fairgrieve (1995) for details).

The size and composition of the four study groups can be compared to other non-study groups which were counted during the course of this study. These were groups encountered and clearly seen during dawn to dusk follows of study groups and other visits to the field. Only counts which were thought to be reasonably accurate have been included. Some groups larger than reported here have been counted by fieldworkers of the Budongo Forest project (A.Plumptre pers.comm.), but the counts presented here probably represent a reasonable estimate of group sizes in the two compartments (Table 6.4).

Table 6.4. Blue monkey group counts for non-study groups (made opportunistically during the study period).

	Compartment N3					*Compartment N15*				
	Adm	**Adf**	**Sub Ad**	**Juv**	**Inf**	**Adm**	**Adf**	**Sub Ad**	**Juv**	**Inf**
	1	5	3	3	0	1	4	3	2	0
	1	4	4	3	0	1	4	4	3	0
	1	3	6	2	0	1	2	1	2	1
	1	3	2	3	1	1	5	3	2	0
	1	5	2	2	0	1	3	2	3	0
	1	4	4	3	1	1	3	2	1	1
	1	4	3	2	1	1	3	3	3	0
	1	3	3	2	0	1	4	2	3	1
	1	4	2	4	0	1	3	2	3	0
	1	3	4	2	0					
	1	3	4	2	0					
Median	1	4	3	2	0	1	4	3	3	0
				Total	**10**				Total	**11**

Table 6.4 shows counts taken throughout the study period of non study groups where the count was thought to be reasonably complete. The median group size for both compartments is very similar and the four study groups (Table 6.3) appear to be representative of groups in each compartment in terms of size and composition.

Scan Sampling Of Groups

A total of 190 dawn to dusk follows were carried out resulting in over 1500 hrs contact with the four groups. Table 6.5 shows a summary of the dawn to dusk follows for each group during each 2 day sample period. Sample periods are referred to by the two week period in which they were carried out eg. July 1 = two days follows from the first two weeks in July. Data are missing for several two day sample periods and some sample periods only resulted in one day's data due to groups being lost or observer illness.

Table 6.5. Summary of contact hours per two day sample period for the four study groups.

	N3 (logged)		*N15 (unlogged)*	
Sample period	N31	N32	N151	N152
July 1	9.5, 8.75	9.25, 8.5	9.25, 9.75	no data
July 2	no data	10.0, 9.5	no data	7.75, 7.75
August 1	8.25, 9.75	no data	9.5, 9.0	no data
August 2	no data	9.0, 8.5	10.25, 9.25	10.0, 8.75
September 1	8.75, 7.0	10.0, 8.75	9.0, 8.0	7, 5.75
September 2	5.75, 7.0	9.25, 9.75	9.25, 8.5	9.75,8.5
October 1	10.25, 8.75	9.0, 8.25	7.75, 10.0	9.5, 8.75
October 2	8.75, 9.75	9.75, 9.75	7.75 *	9.5, 9.5
November 1	9.75, 11.5	11.25, 11.0	10.75, 8.0	9.5, 8.25
November 2	10.75, 11.25	10.25, 10.0	7.5, 9.75	10.75, 9.5
December 1	11.0, 10.0	9.25, 11.0	10.0, 10.5	10.0, 8.25
December 2	11.5, 9.75	11.0, 10.5	5.25, 8.75	no data
January 1	no data	11.25, 7.75	8.75, 10.0	no data
January 2	9.5, 11.5	11.25, 7.75	5.0 *	7.25, 8.0
February 1	9.25 *	8.75 *	10.5, 8.25	9.75 *
February 2	10.5, 10.25	10.75, 8.75	10.5, 10.5	10.0, 8.0
March 1	11.25, 9.25	9.75, 9.5	8.75, 9.25	9.0, 10.0
March 2	10.75, 11.0	11.0, 11.5	11.5, 11.0	7.25, 10.0
April 1	10.0, 9.75	10.25 *	9.0, 10.25	7.25, 6.25
April 2	10.75, 9.0	6.5, 5.5	6.25, 7.0	9.5, 8.0
May 1	8.75, 9.5	9.25, 9.0	9.5, 9.75	10.25, 9.0
May 2	7.25, 9.75	9.75, 10.75	10.75 *	no data
June 1	5.75 *	10.25, 10.0	10.25, 10.0	10.0, 9.0
June 2	9.75, 10.0	10.25, 10.5	no data	9.5, 8.5

* = only one day's follow completed.

The number of days' contact and total hours' contact differed slightly for each group (Table 6.5). The mean number of hours contact per day with each group is shown in Table 6.6 together with the total number of days sampled and the total contact hours. Groups in the unlogged compartment were followed for slightly fewer contact hours in total and mean contact hours per day were slightly lower.

Table 6.6. Summary of dawn to dusk follows carried out.

Compartment	*Group*	*Total no. days*	*Mean contact hrs/day (stdev)*	*Total hrs contact*
N3 (Logged)	N31	40	9.53 (1.44)	381.25
	N32	44	9.68 (1.22)	426.25
N15 (Unlogged)	N151	41	9.13 (1.46)	374.5
	N152	37	8.79 (1.19)	325.25
	Total	190	------	1507.25

Scans from the four groups were distributed throughout the day in a similar pattern (Figure 6.3) and despite attempts to locate individuals even when resting, fewer scans were recorded for all groups in the early afternoon. Despite this reduction in the number of completed scans in the early afternoon, the sampling allows comparable estimates of diurnal ranging, activity and feeding patterns.

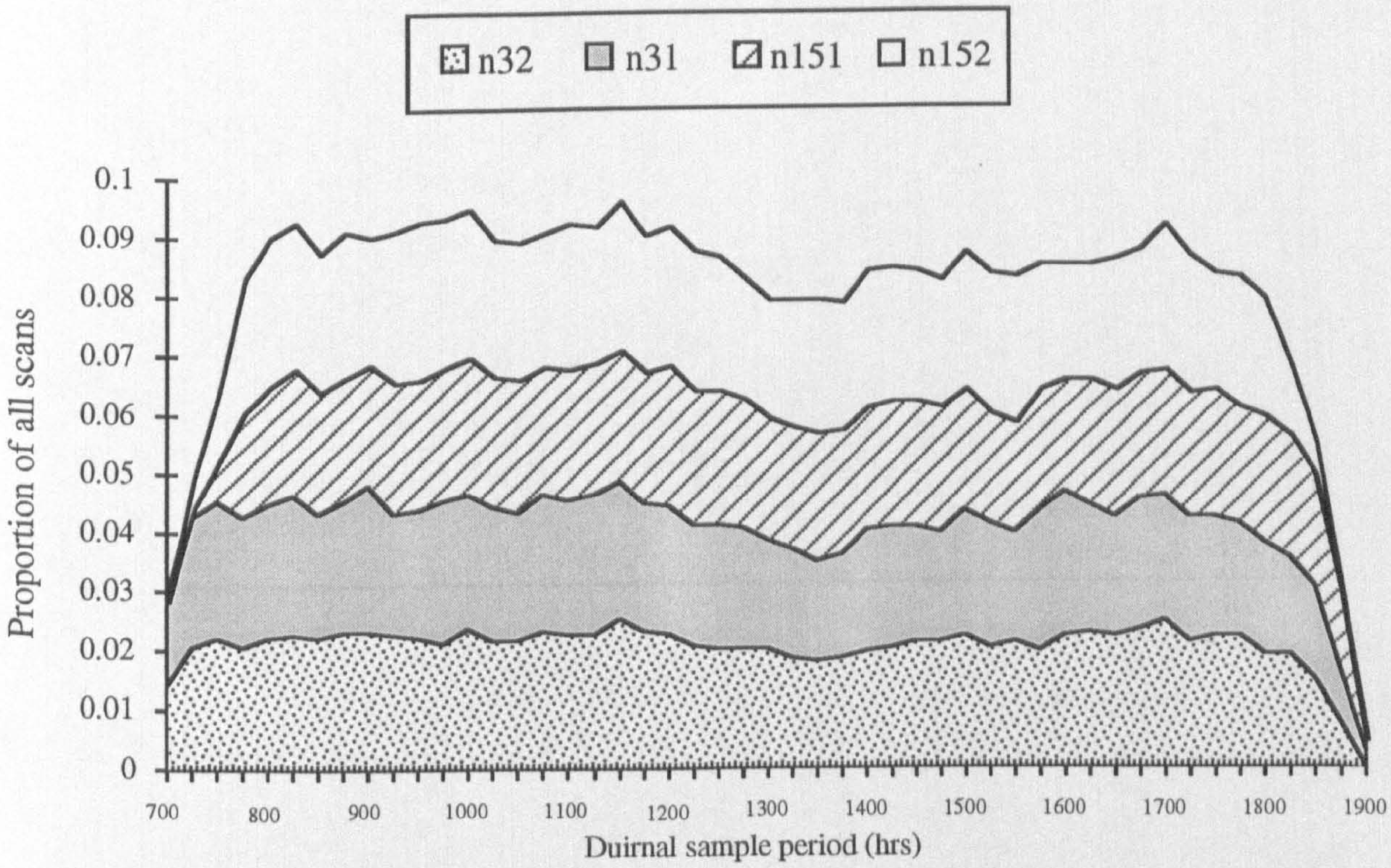


Figure 6.3. Proportion of completed scans (as a proportion of total scans per day) from each 15 min sample period from 7am to 7pm.

Age-Sex Class Sampling And Correction Factors

Although the sampling technique was designed to give a random selection of individuals within the group, it was found that in some cases, certain age-sex classes were sampled more often than would be expected by chance (Table 6.7). Chi square tests were carried out between observed frequency of individuals sampled in each age class and the expected frequency based on group composition. Results indicated that some age-sex classes were sampled more frequently than would be expected if random sampling was occurring (Table 6.8). This was probably due to some age-sex classes being more conspicuous therefore being scanned disproportionately more frequently (eg. females, who normally formed the core of the group; males who had a larger body size).

Table 6.7. Observed and Expected frequencies of scans for different age-sex classes.

	Group	*Males*	*Females*	*Sub-adults*	*Juveniles*	TOTAL
Obs.	N32	595	2757	2019	2325	7696
Exp.	N32	705	2820	2115	2056	7696
Obs.	N31	659	2600	1813	1618	6690
Exp.	N31	669	2555	1946	1520	6690
Obs.	N151	695	2784	1819	1884	7182
Exp.	N151	611	2699	1936	1936	7182
Obs.	N152	476	2153	1247	1411	5287
Exp.	N152	538	2153	1469	1126	5287

Table 6.8. Chi square values testing between observed and expected frequencies of scans for age-sex classes:

Group	*Males*	*Females*	*Sub-adults*	*Juveniles*
N32	17.15 ** less	1.40 ns	4.35 ns less	35.14 ** more
N31	0.14 ns	0.81 ns	9.11 * less	6.258 ns
N151	11.47 ** more	2.63 ns	7.02 ns	1.374 ns
N152	7.25 * less	0.0004 ns	33.44 ** less	72.17 ** more

Significance levels(df=3): *= $P < 0.05$, **=$P < 0.01$, ns= $P > 0.05$
"less" signifies sampled less than expected.
"more" signifies sampled more than expected.

Sub adults were sampled less than expected in three groups and juveniles more than expected in two groups. Adult males were sampled more than expected in group N151 and less than expected in N32 and N152 (Table 6.8). Therefore, to allow direct comparison of the four groups it was necessary to apply correction factors to feeding and activity data. Totals and proportions (for activity categories and feeding scores) were calculated for each age-sex class separately and then multiplied by a correction factor which accounted for the difference between expected scans for that age-sex class (calculated from group counts) and the observed scans. Then the corrected proportions for age-sex classes were summed to give overall proportions for groups.

6.4 DISCUSSION

Population density

The overall density of blue monkeys in Budongo forest lies at the middle to lower end of the range of densities reported from other sites (See Table 2.1, Chapter 2). The Budongo estimate includes a range of compartment estimates from 7.7 ind/km^2 to 85.9 ind/km^2 (Plumptre et al. 1994). It is noticeable that even the highest of these estimates is considerably lower than the 183 ind/km^2 reported for Budongo by Aldrich-Blake (1970). However, Aldrich-Blake's estimate was made by extrapolating home range size estimates from only a small part of the forest and it may therefore be inaccurate.

As reported by Plumptre and Reynolds (1994), there are almost twice as many blue monkeys per km^2 in the logged compartment (N3) compared to the unlogged compartment (N15). The difference in density between these two compartments (31.2 ind/km^2 vs. 57.5 ind/km^2) is smaller than the difference between all logged compartments and all unlogged compartments (15.6 ind/km^2 vs. 58.2 ind/km^2). This is partly due to a very low density estimate for blue monkeys in the second unlogged compartment (KP 15: A.Plumptre unpubl.data). The other two arboreal species of primate (*Cercopithecus ascanius, Colobus guereza*) show disproportionately lower densities in unlogged forest and this results in a much higher ratio of individuals of these two species to blue monkey individuals in logged forest. Plumptre and Reynolds (1994) found the density of *C.mitis* and *C.ascanius* to be positively correlated which is not surprising due to the similar dietary tendencies of these two species (Cords 1986a, Struhsaker 1978).

Determinants of primate species diversity and density in natural forest sites include historical/zoo geographical factors, levels of competition, mortality rates as well as habitat heterogeneity and food availability (Oates et al 1990, Struhsaker 1981). It is also likely that blue monkey densities from other sites reflect different levels of inter specific competition and food availability (Cords 1987, Struhsaker 1978). Lawes (1992) presents a positive correlation between samango (*C.mitis erythrarchus*) density and tree species diversity (per 0.1 ha) but proposes that at a certain level of tree species diversity, food trees become dispersed to the extent that problems of obtaining food preclude high densities. In contrast to this study, Butynski (1990) reported more variation in blue monkey density between areas with similar primate communities and similar vegetation, compared to areas with extremely different primate communities and different vegetation. He concluded therefore that differences in the primate community and habitat were not large enough to account for the observed differences in blue monkey density. As an alternative hypothesis, he proposed that the low density population had gone through a 'bottleneck' in population density due to a disease outbreak. The evidence from this study supports the hypothesis that blue monkey density is more likely to be determined by habitat differences and does not support Butynski's disease hypothesis. Inter specific competition may be higher in logged forest due to slightly higher relative densities of *C.ascanius* and *Colobus guereza* , but the balance of competition is probably redressed by the higher food availability (See Chapters 6 and 7). There are no other differences in the species composition of the two primate communities in N3 and N15 which could account for the observed difference in blue monkey density.

Previous studies have reported a reduction in primate densities immediately following logging (Skorupa 1986, White 1992, 1994b). Some of these studies however, have failed to consider different habitat types within the forest separately (see Johns and Skorupa (1987) for a review). There is also recent evidence that in the long term subsequent to logging, especially where logging intensity is not excessively high, primate density increases are common (Grieser Johns and Grieser Johns 1995, Plumptre and Reynolds 1994). As has been show in this study, it is emerging that responses of primates and other wildlife are also dependent on the type of vegetation present prior to logging (Plumptre and Reynolds 1994, this study). It is interesting to note that at Kakamega Forest, Kenya which has one of the highest blue monkey densities previously recorded was in fact partially felled in the 1940's and has a heavy undergrowth, low canopy and high species diversity (Cords 1987).

Finally, Butynski (1990) warns against making the assumption that a primate population being studied is at carrying capacity. Despite this commonly made assumption, he points out that primate populations may frequently be below carrying capacity and our understanding derived from studies of such populations may be inaccurate. Although such an assumption is almost impossible to test, the presence of neighbouring blue monkey groups on the edges of study group ranges in both areas and the observed difference in density (logged vs. unlogged) across the whole forest suggest that this assumption is likely to be met.

Group Size/Demography

There appears to be no real difference in group size or composition between the two compartments, and the study groups seem to be representative of groups in general. The range of group sizes observed in this study (10-13 individuals) agrees is similar to those reported by Aldrich-Blake (1971: mean group size for Budongo = 13.3 individuals per group, Range: 12-17). The group sizes reported here are smaller than groups reported from some other sites (Cords 1988, Lawes 1991, Rudran 1978) and appear to be at the lower end of the group size spectrum for blue monkeys (Figure 6.9). However, recent counts of three of the four study groups carried out by field assistants working for the Budongo Forest Project show increases in group size for both groups in logged forest, but little change for the one group counted in unlogged forest (Table 6.9, A.Plumptre pers. comm.). This suggests that groups in logged forest may have a higher birth rate (see below) and may be undergoing an increase in group size.

Table 6.9 Group size estimates for study groups June 1993 to September 1995 (data from this study and A. Plumptre unpubl. data)

	Group Size		
Group	*June 1993*	*June 1994*	*September 1995*
N32	11	12	17
N31	10	12	18
N151	12	15	16
N152	12	12	??

Plotting group size against range size from previous studies of blue monkeys (Figure 6.9) there is a positive correlation between group size and range size across a variety of habitat types (Spearmann rank correlation r=0.68, p<0.01). The two outlying points in the lower right hand side of the graph were excluded from this analysis as they represent i) the C.*mitis* group at the extent of it's Southern range (Lawes and Piper 1992) and ii) an unusually large group formed as a result of fission (Cords and Rowell 1986b).

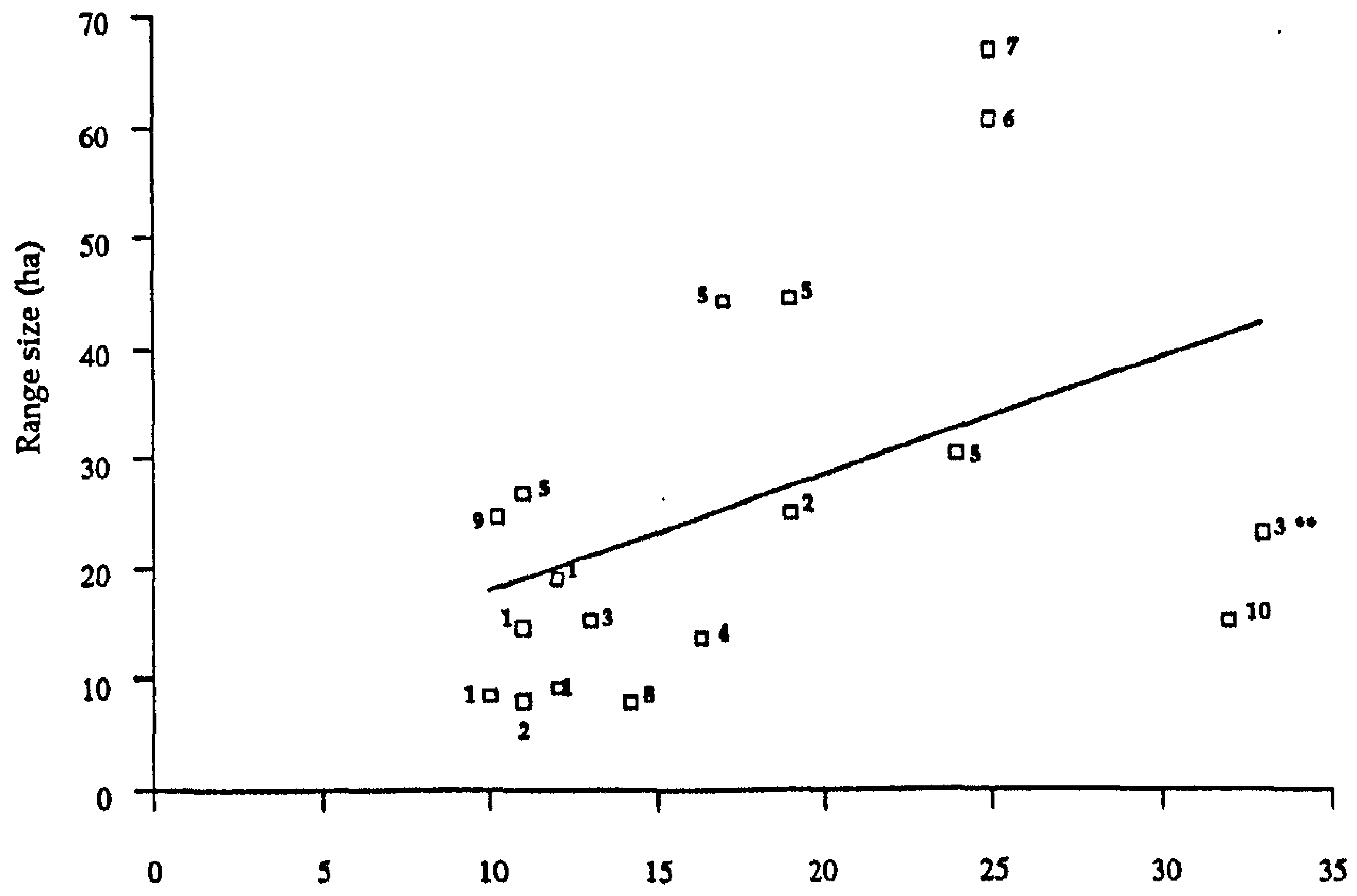


Figure 6.4. The relationship between group size and range area (ha) in blue monkeys where previously studied.

Key:1: This study, 2: Beeson (1985), 3:Cords and Rowell (1986) , 4: Devos and Omar (1971), 5: Butynski (1991), 6: Struhsaker (1978), 7: Rudran (1978), 8:Aldrich-Blake (1971), 9: Schlichte (1978), 10: Lawes and Piper (1992)

Larger groups spend more time moving and searching for food for all of their members therefore large groups would not be expected where food availability is low. However, group size may also reflect the nature and distribution of food patches: for a habitat with evenly dispersed but small food patches which vary over time, a small group size would be expected. If the habitat is poorer quality with large resource patches distributed unevenly throughout then larger groups size might be observed. Van Schaik and Hostermann (1994) also discussed the importance of predation in determining group size but concluded that for guenons, the formation of mixed-species associations probably served as a predator avoidance mechanism and precluded the need to increase the number of adult males (ie precludes an increases in group size). It is likely therefore, that the small groups observed in Budongo reflect the even distribution and constant availability (in space and time) of food resources in the habitat. All four groups show the same one male, matrilineal group structure reported in other sites (Andelman 1986, Cords 1988).

Demographic changes recorded in the 14 month period for which group counts were available were probably too few to provide any insight into differences in demographic patterns between the two compartments. Births did appear to be seasonally clumped in all four groups, 7 out of a total of 10 infants being born in the period November-March. This agrees with previous studies which stated that although births can occur throughout the year they are likely to be clumped especially where climatic conditions show strong seasonality (Gevaerts 1992, Rowell and Richards 1979). This peak in births was observed some 2-5 months before the onset of the long rains (a period of high food availability: Chapter 6). The only discernible differences were a higher number of births per female in both groups in N15 and one male take-over in the group N32 compared to no take-overs in all the other groups. As stated above, subsequent to this study, groups in N3 have recently shown an increase in group size which may indicate a higher reproductive output as a result of higher dietary quality and a suitable habitat with a constant availability of food (See Chapters 7 and 9).

Butynski (1990) reported a higher birth rate in a low density *C.mitis* population but pointed out that this may have been due to higher levels of infant mortality rather than a high population growth rate. In addition, he concluded that the low density population was recovering from a historical disease outbreak and was not yet at carrying capacity. As no cases of mortality were observed during this study (except one infanticide) it is difficult to make any conclusions regarding the comparative birth rates. Johns (1981) did observe an increase in infant mortality in *Hylobates lar* and *Presbytis melalophos* following logging but was unable to determine the exact cause. He suggested increased mortality (abandonment, falls and predation) or a reduction in food quality leading to reduced lactation.

Mixed Species Association

The four study groups spent between 14 and 22 % of all scans in association with C. *ascanius* . This is less than reported by Cords (1987) in Kakamega where the population density is higher and group size larger for both C.*mitis* and C.*ascanius* . However, in Kibale forest where density and group size are similar to those in Budongo (although levels of inter specific competition are higher) groups of blue monkeys spent similar amounts of time in association with redtails (Range: 0-29 %, Mean = 13 %; Rudran 1978). There was no difference between N3 and N15 in the proportion of all scans where groups were recorded in association with C. *ascanius* . However, given the lower ratio of C. *ascanius* : C.*mitis* (groups and individuals) in unlogged forest, it seems groups in unlogged forest are spending more time in association with redtails relative to their abundance. Cords (1987) concluded that redtails were mainly responsible for the formation and persistence of mixed species groups with blue monkeys in order to enhance food exploitation. The higher incidence of mixed species association in N15 may be a consequence of the distribution and abundance of food resources in unlogged forest (See Chapter 7 and 8). It is unlikely that there are any differences in predation pressure between the two sites as the major predator - the Crowned Hawk Eagle (*Stephanoaetus coronatus*) - ranges over areas of several km^2 (Struhsaker and Leakey 1990) and occurred in both sites.

Intra-and Inter-specific Interactions

There is some degree of overlap between study groups and non-study groups of blue monkeys in both N3 and N15 although the degree of overlap appears to be less in unlogged forest. The number of *C.ascanius* and *Colobus guereza* groups overlapping or adjacent is higher in logged forest as a result of the relative higher density of these species. Overall it is likely that the degree of intra-specific territoriality and competition (inter- and intra-specific) may be slightly higher in logged forest. As discussed above, quantifying the level of inter specific competition is difficult, but it is unlikely that differences in levels of competition are the proximate causes of differences in density between N3 and N15. If there are higher levels of interspecific competition in N3, this may even cause a reduction in density as determined by food availability.

Conclusions

i)Population density differs between logged and unlogged forest for blue monkeys and two other arboreal species of primate.

ii)Group size does not appear to differ although the lack of long term demographic data does not allow to assess the dynamics of groups in the two compartments.

iii) Group size in Budongo appears to be smaller than in other sites suggesting high food availability and regular dispersal of food resources within the habitat.

iv) All four groups spent similar amounts of time in association with groups of redtail monkeys although relative to the density of this species in the two compartments, groups in unlogged forest spent a higher proportion of time in association.

CHAPTER 7

DIETARY COMPOSITION

7.1 INTRODUCTION

Dietary quality is important in determining female fecundity and hence population growth rate in many primates (Chapman and Fedigan 1984, Milton 1982). In addition, overall carrying capacity or population density in a habitat is thought to be determined by food availability, with special emphasis on periods of food shortage (eg 'dry season bottlenecks': Cant 1980, Oates et al. 1990, Terborgh 1986). Changes in diet observed in a primate community following logging may therefore influence the nutritional intake and reproductive rate. These factors may be important in determining carrying capacity of logged forest and result in a change in population density of the resident primate species. It is widely believed that the response of a primate species will be dependent on the breadth of its feeding niche and dietary flexibility, species with a higher degree of dietary flexibility exhibiting less change in population density (Johns 1985c, Skorupa 1986). Dietary shifts in undisturbed forests due to seasonal changes in food availability can give an indication of potential responses to logging. Such changes in foraging patterns and food intake have been previously documented (Leighton and Leighton 1983, Rudran 1978), although detailed studies of dietary shifts due to logging are few (but see Johns 1988a). In addition to food tree density and seasonal availability, food preferences are an important factor in determining primate diet (Gautier-Hion 1988).

There is a reasonably large amount of background information available on the composition of blue monkey diet in a range of habitats (Beeson 1985, Butynski 1990, Cords 1986, Lawes 1991, Maganga and Wright 1992, Rudran 1978). Variation in dietary composition has been recorded between sites and between groups within the same site, the most variable component of diet being the proportion of fruit. Normally the major component of the diet by proportion of feeding scores is fruit which may also be the most nutritionally rewarding component of the diet (Lawes 1991, Richard 1985). The remainder of the diet is made up of other items such as young leaves, invertebrates or flowers (Beeson 1989, Butynski 1990, Gautier-Hion 1988, Schlichte 1978). These supplementary parts of the diet also vary between populations (Lawes 1991).

There is some debate as to the potential role of blue monkeys as seed dispersal agents, with different conclusions being reached in different studies. As with other Old World monkeys, blue monkeys make extensive use of cheek pouches to process and discard seeds (Corlett and Lucas 1990) but there is some evidence of seeds being swallowed and passed intact (Kaplin pers.comm., this study). However, Wrangham et al. (1994) and Rowell and Mitchell (1991) classify blue monkeys as seed destroyers with a limited role as seed dispersers. In an attempt to investigate further the seed processing strategies of blue monkeys and their contribution to seed dispersal in Budongo Forest, collection and analysis of dung samples was carried out.

7.2 METHODS

Correction of Feeding Data

Feeding records from dawn to dusk follows (24 two week periods) were used in analyses of dietary composition and variation. As discussed in Chapter 4, scan sampling resulted in some age-sex classes being sampled more than would have been expected with fully random sampling. Previous studies have shown significant differences in dietary composition between different age-sex classes in *C.mitis* (Cords 1986, Lawes 1991). Correction factors were therefore applied to feeding data to reduce the bias due to over sampling particular age-sex classes and allow direct comparison between groups. Data were first separated into age-sex classes, and feeding scores for a particular food item calculated. These figures were then divided by the total number of feeding scores for that age-sex class from the two day sample period to give an uncorrected proportion. This uncorrected proportion was then multiplied by the expected number of feeding records for the age-sex class to give a corrected score for that age-sex class feeding on a particular plant food item. The expected number of feeding scores was calculated by multiplying the total number of feeding scores for the group by the proportion of the group that the age-sex class represented (taken from group counts). Corrected scores for each age-sex class were then summed and proportions for plant food items were calculated for each group. These corrected proportions were then compared for the overall study period and by bi-weekly sample periods. Proportions of all fruit and all leaves were calculated initially, and then ripe fruit/unripe fruit and mature leaves/young leaves were considered separately for further analyses.

Dietary Overlap, Diversity and Evenness

Dietary overlap between all four groups was calculated using the method of Holmes and Pitelka (1968) in which shared proportions of dietary items are summed. For each two day sample, Shannon-Weiner indices of dietary diversity were calculated using $H = -\Sigma\, p_i \ln p_i$ where p_i is the proportion of feeding scores for species item i in the diet (Pielou 1966). Evenness in use of dietary items was also calculated as $J = H/\ln N$ where N is equal to the total number of items in the diet.

Important Food Items

Previous studies have reported that a relatively small number of important food items make up a high proportion of total food intake in blue monkeys. Therefore, the top twenty plant food items by proportion of feeding scores were determined and compared between groups and compartments for the whole study period. In addition, for each bi-weekly sample period, the top 5 plant food items by proportion of feeding scores were determined. This gives an indication of the items that were regularly and consistently used. For these analyses, ripe/unripe fruit and mature leaves/young leaves were considered separately.

Distribution and Abundance of Important Food Species

Importance Values and Coefficients of Dispersion (Greig Smith 1983) were compared for the top 10 food species to give an indication of the distribution and abundance of important food trees in the two ranges (see Chapter 4 for description of Importance Values). The Coefficient of Dispersion gives an indication of departure from random for the distribution of a particular tree species. If a species is dispersed randomly in a Poisson distribution, the Coefficient is 1. A coefficient of less than 1 suggests a regular, over dispersed distribution and if greater than 1, a clumped pattern. As it can only be calculated for species which are neither very rare or very common (Greig Smith 1983) the following trees were excluded from Coefficient of Dispersion calculations - N3 : *Celtis durandii, Celtis mildbraedii, Ficus sansibarica* ; N15 : *Cynometra alexandri, Celtis mildbraedii, Ficus lingua, Alaphia landolphioides (climber).*

Selection ratios (sensu Lawes et al. 1990) were calculated to investigate how groups in the two compartments were feeding on food items in relation to their availability. Proportional availability of particular items was calculated using the proportional basal area for the tree species within the range and the production score for the two week sample period (See Chapter 6).The proportion of feeding scores for that food item was then divided by its proportional availability. Therefore a ratio of 1 would indicate that a food item is being eaten in direct proportion to its availability. A ratio of less than 1 would indicate a food item being eaten with lower frequency than its availability would suggest. A ratio of higher than 1 indicates that a food item is being eaten with a higher frequency than its availability would suggest. Although this index does not take into account factors like the nutritional quality of the food item or the availability of alternative foods, it provides a relative index which can then be used to compare dietary selection in the two groups.

Seasonal Diet

Although the data were not complete for all groups, seasonal patterns in diet were examined by plotting the proportion of different food categories per two day sample period. Where data were missing, mid values were used. Ripe/unripe fruits and young/mature leaves were pooled for this analysis.

Seed Dispersal

Dung samples were collected opportunistically during dawn-to-dusk follows and on other visits to the field only when it was certain that the sample came from a blue monkey. Due to the distance some samples fell through the canopy before reaching the ground, some of the samples broke up and were therefore incomplete but still collected. Collected samples were washed through a sieve (1 x 1mm mesh) and all intact seeds were removed, counted and identified. Presence of fragments of seeds was noted but due to difficulty of identifying seeds from fragments alone, fragments were not identified or quantified. Where seeds could not be identified, a specimen was dried and kept for reference. Some of these unidentified seeds could later be identified by comparing seeds from ripe fruits collected in the field. Commonly found seeds were also measured to give an estimate of seed size.

7.3 RESULTS

Overall Diet

In common with the findings of previous studies on blue monkeys feeding activity in all groups was concentrated in the early morning and late afternoon with some seasonal variation in this general pattern being observed. The dietary composition of all four groups was also broadly similar to blue monkey diets recorded in previous studies (Beeson 1985, Butynski 1990, Cords 1986, Lawes 1992, Rudran 1978). The main component of the diet consisted of fruit, but all groups also included young leaves, flowers, buds and shoots in the diet. Other rare foods eaten include fungus, guinea fowl eggs, snails, lichen and on one occasion, a male from a non-study group of blue monkeys was observed eating a flying squirrel (Lord Derby's flying squirrel : *Anomalurus derbianus*), which it was presumed he had caught since the remains were still soft when he finished eating and dropped them. Previous studies have also recorded meat eating in C.*mitis* (Butynski 1982a, Cordeiro 1994, Wahome et al 1988).

A full list of plant parts eaten by the four groups is listed in Appendix 2 and the four groups together used 170 different items from a total of 68 different tree species. Each single group used between 39-40 different species and 85-87 different items (Table 7.1) but there were no differences in the number of species or items used overall.

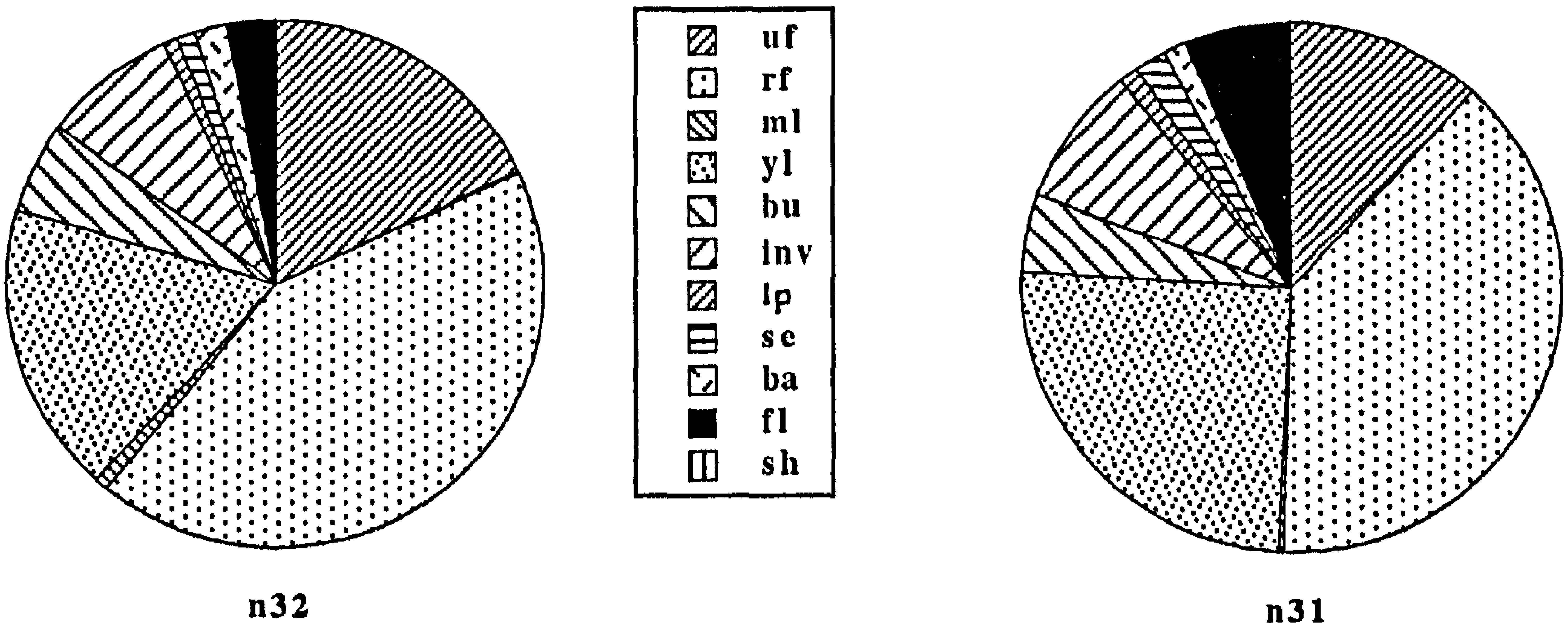
Table 7.1. Feeding scores, items and tree species used as food by each group

Group	*Total no. of scans feeding*	*No. of items used*	*No. of spp. used*
N31	*2757*	*87*	*43*
N32	*2360*	*85*	*40*
N151	*2955*	*87*	*39*
N152	*2365*	*86*	*40*
TOTAL	10437	170	68

Comparing the dietary composition between logged and unlogged compartments, some differences in the overall composition by categories were observed (Figure 7.1.a to 7.1.d).

LOGGED

Figure 7.1.a. **Figure 7.1.b.**



UNLOGGED

Figure 7.1.c **Figure 7.1.d**

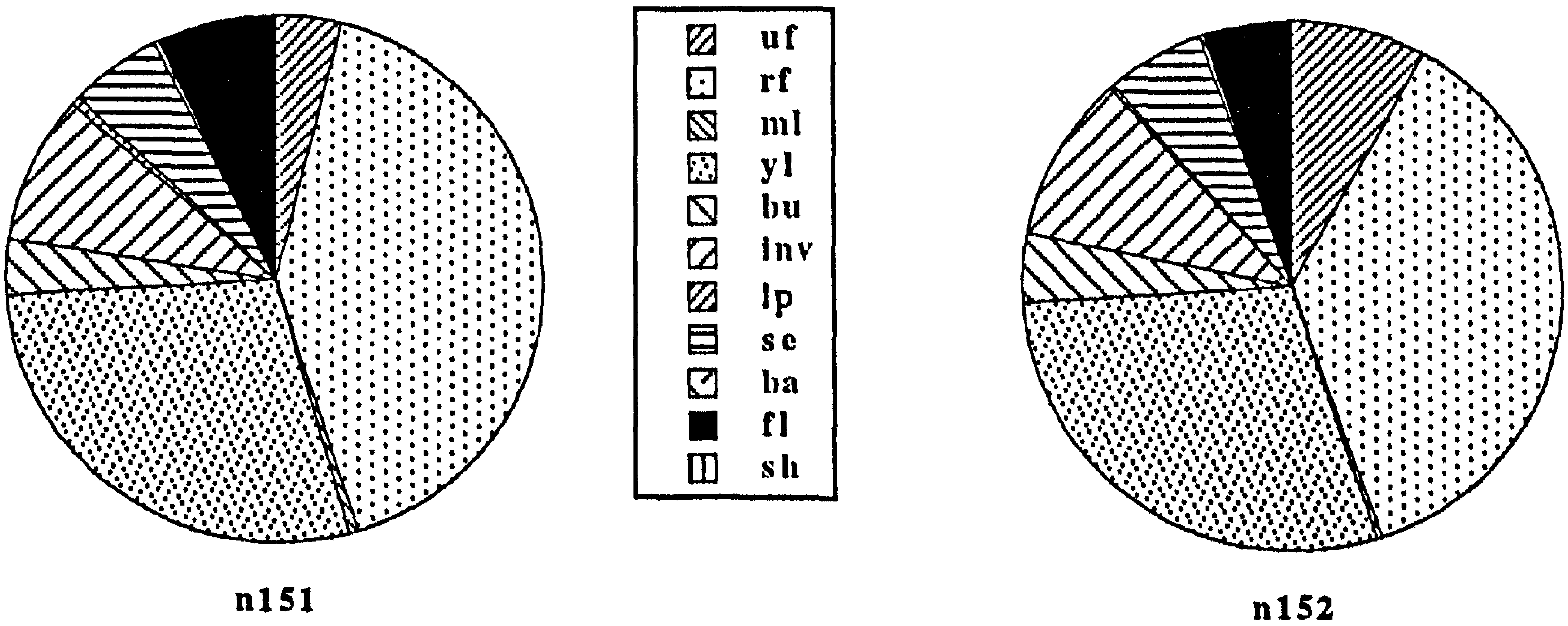


Figure 7.1.a to 7.1.d Overall dietary proportions for four groups (a.N31/b.N32: logged forest c.N151/d.N152: Unlogged forest (see Table 7.2 for values)

Firstly, both groups in the logged compartment have a higher proportion of feeding scores for unripe fruit and ripe fruit(Figure 7.1.a and 7.1.b). Both groups in unlogged forest have a much lower intake of unripe fruit and a lower intake of ripe fruit and as a consequence supplement the fruit component of their diet by including a higher proportion of young leaves, invertebrates, seeds and flowers (Figure 7.1.c and 7.1.d).

Proportions for each item category were also calculated for each two day sample period and a Kruskal Wallis analysis of variance was carried out to test for variation in the proportion of feeding scores in different categories (X^2 values shown in Table 7.2). There was significant variation in the proportion of unripe fruit in the diet ($X^2=21.88$, $P<0.01$). Both groups in N3 show a significantly higher proportion of unripe fruit in the diet compared to groups in N15 . There was also significant variation in the proportion of seeds and bark in the diet (seeds: $X^2=23.73$, $P < 0.001$; bark $X^2=23.78$, $P < 0.001$). Both groups in N3 show a significantly lower proportion of seeds but a significantly higher proportion of bark (which was obtained mainly from *Khaya anthotheca* and *Albizzia spp)* .Both groups in N15 also showed a higher but non-significant proportion of leaves and invertebrates in the diet (Table 7.2)

Table 7.2. Proportion of all feeding scores for different food categories and X^2 values for Kruskal Wallis analysis of variance.

CATEGORY	N32	N31	N151	N152	X^2		
Unripe fruit	0.179	0.119	0.038	0.081	21.88	***	N3>>N15
Ripe fruit	0.429	0.389	0.413	0.366	3.03	ns	
Mature leaves	0.008	0.004	0.004	0.003	3.18	ns	
Young leaves	0.174	0.250	0.285	0.287	5.44	ns	N15>N3
Buds	0.056	0.044	0.033	0.043	1.71	ns	
Flowers	0.028	0.063	0.073	0.051	2.78	ns	N15>N3
Invert.	0.085	0.086	0.091	0.102	6.33	ns	N15>N3
Seeds	0.011	0.018	0.056	0.062	23.73	***	N15>>N3
Shoots	0.010	0.012	0.005	0.003	4.76	ns	
Bark	0.020	0.015	0.002	0.002	23.78	***	N3>>N15

ns = not significant, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$

Combining data for compartments, differences between groups in logged and unlogged forest are significant by Mann Whitney U test for unripe fruit ($z=3.53$, $P<0.01$), seeds ($z=3.85$, $P<0.01$) and bark ($z=3.85$, $P<0.01$).

Seasonal diet

The seasonal patterns of feeding on different food categories for the four groups are shown in Figures 7.2.a to 7.2.d. The main component of the diet throughout the 12 month study period was fruit for all four groups, supplemented by leaves, invertebrates and flowers. The presence of flowers in the diet of the groups in logged forest is much more variable and seeds feature very rarely in the diet of both groups in logged forest as compared to groups in unlogged forest. Group N32 spent a small amount of time feeding on flowers but did regularly spend time feeding on buds of *Ficus spp* (Figure 7.2.a). Group N31 shows a very high proportion of flowers around February due to a large amount of time spent feeding on the flowers of one tree species (*Chrysophyllum albidum*), several individuals of which were flowering within the group's range at this time (Figure 7..2.b). This pattern of feeding may have been somewhat unrepresentative. Bark (*Khaya anthotheca* and *Albizzia* spp.) featured in the diet of both group N31 and

N32 at certain times of the year but very infrequently in the diet of groups in N15. Both groups in unlogged forest show a much higher variation in the proportion of fruit in the seasonal diet and this variable intake of fruit is supplemented by a more constant intake of flowers, leaves and seeds (Figures 7.2.a and 7.2.b). Bark is only rarely included in the diet of both group N151 and N152. Peaks in flower intake occur in both groups mainly due to feeding on flowers of *Chrysophyllum albidum* , *Entandrophragma* sp. and *Cynometra alexandri* .

LOGGED FOREST (N3) GROUPS

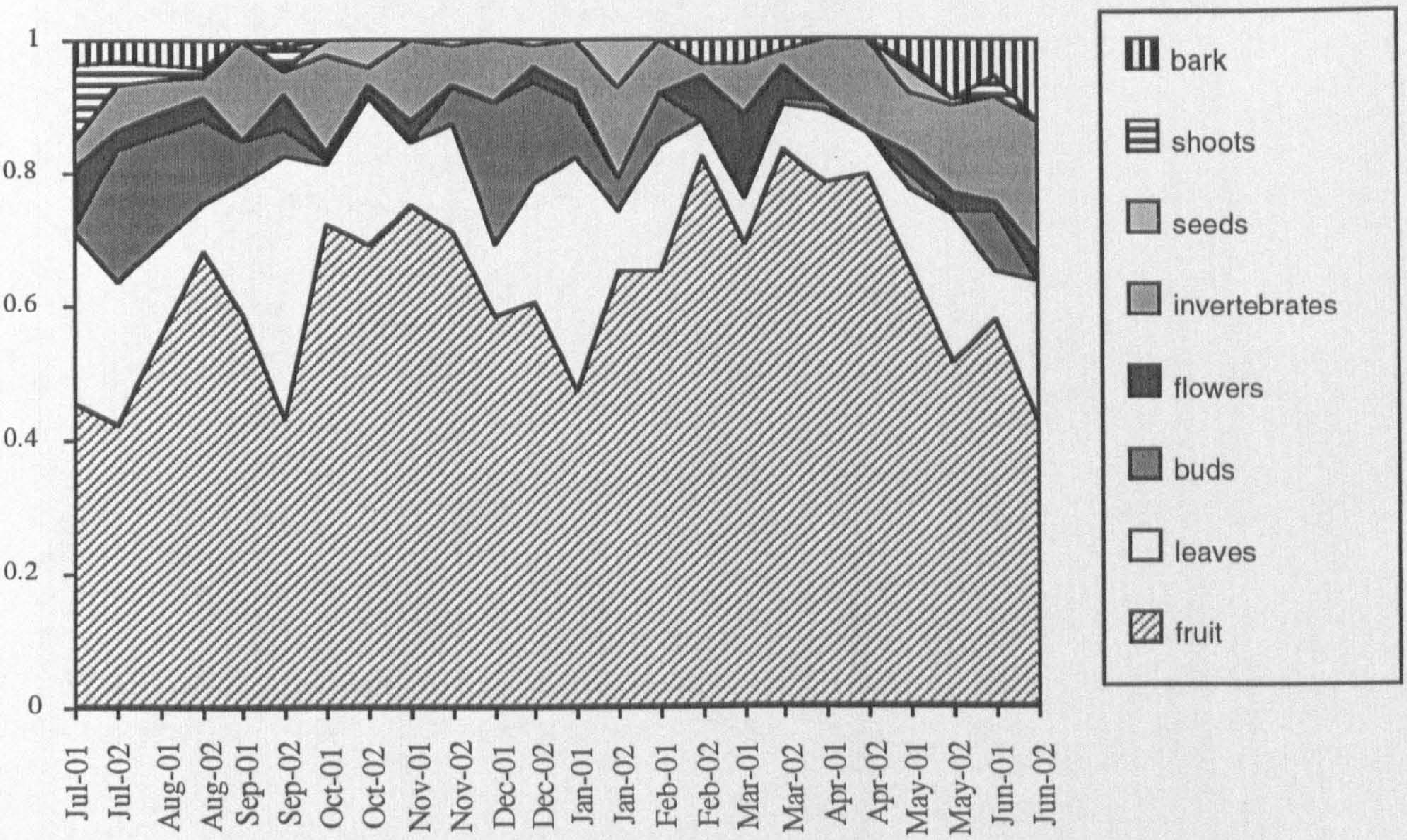


Figure 7.2.a. GroupN32 Seasonal dietary composition

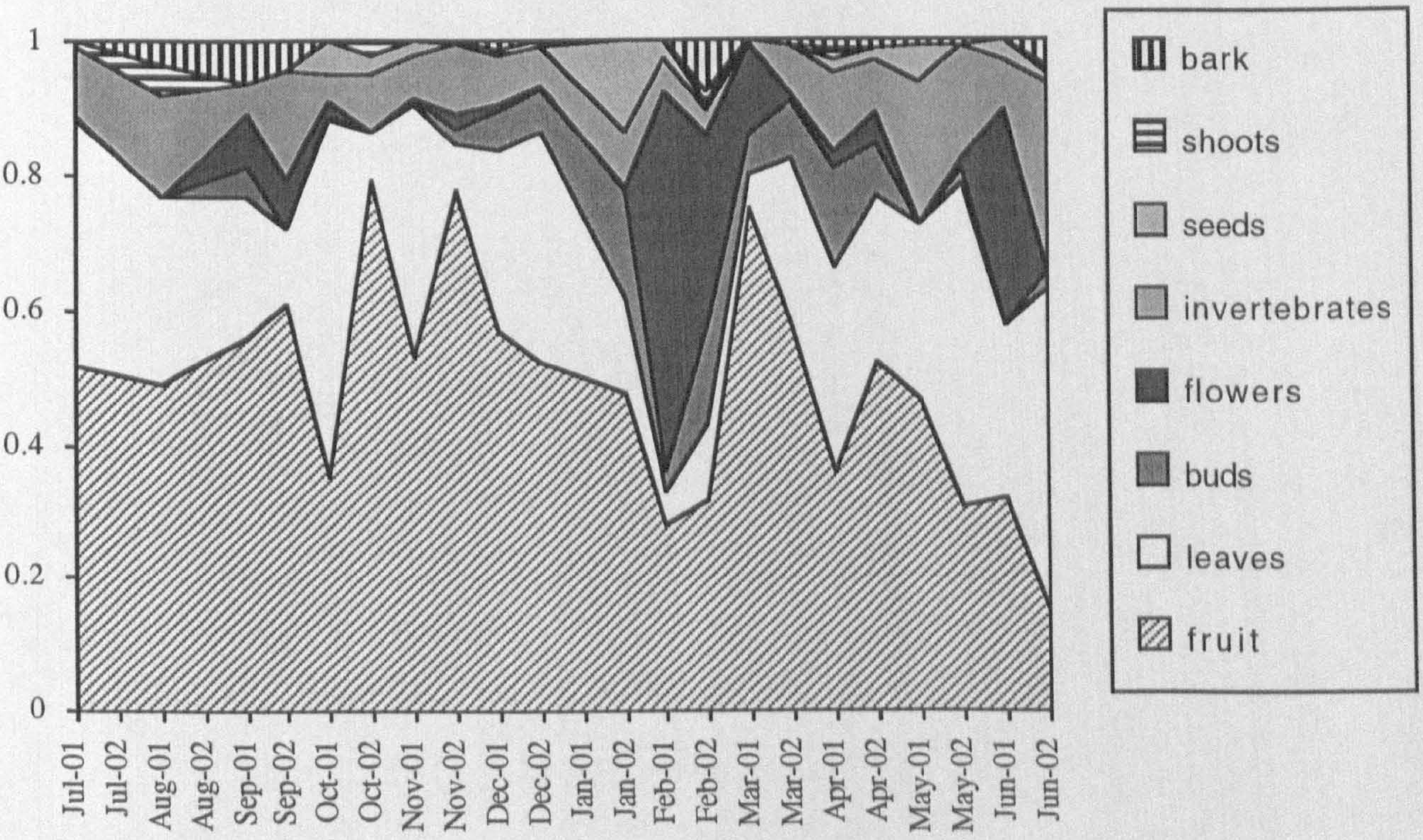


Figure 7.2.b. GroupN31 Seasonal dietary composition

UNLOGGED FOREST (N15) GROUPS

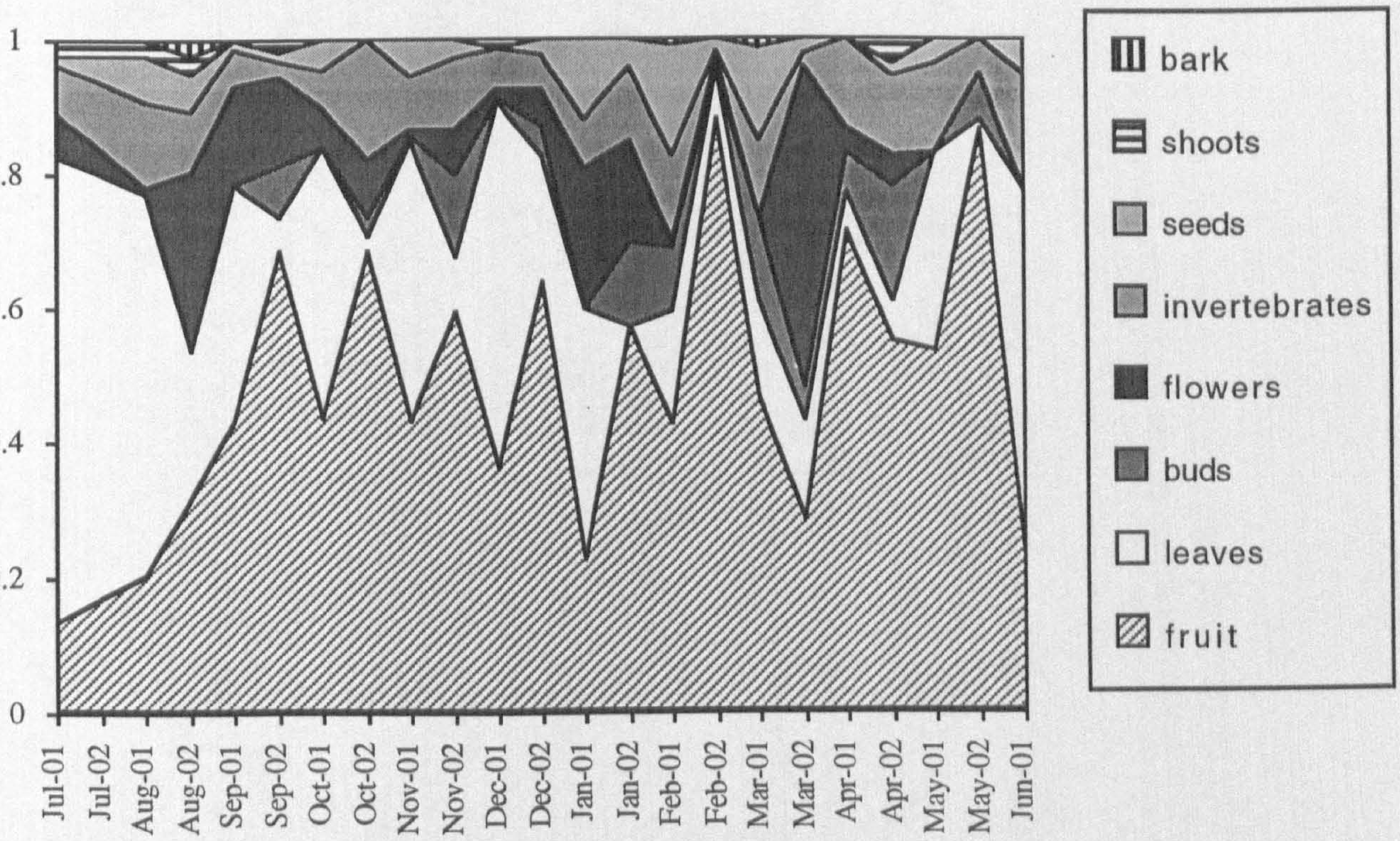


Figure 7.2.c. Group N151 Seasonal dietary composition

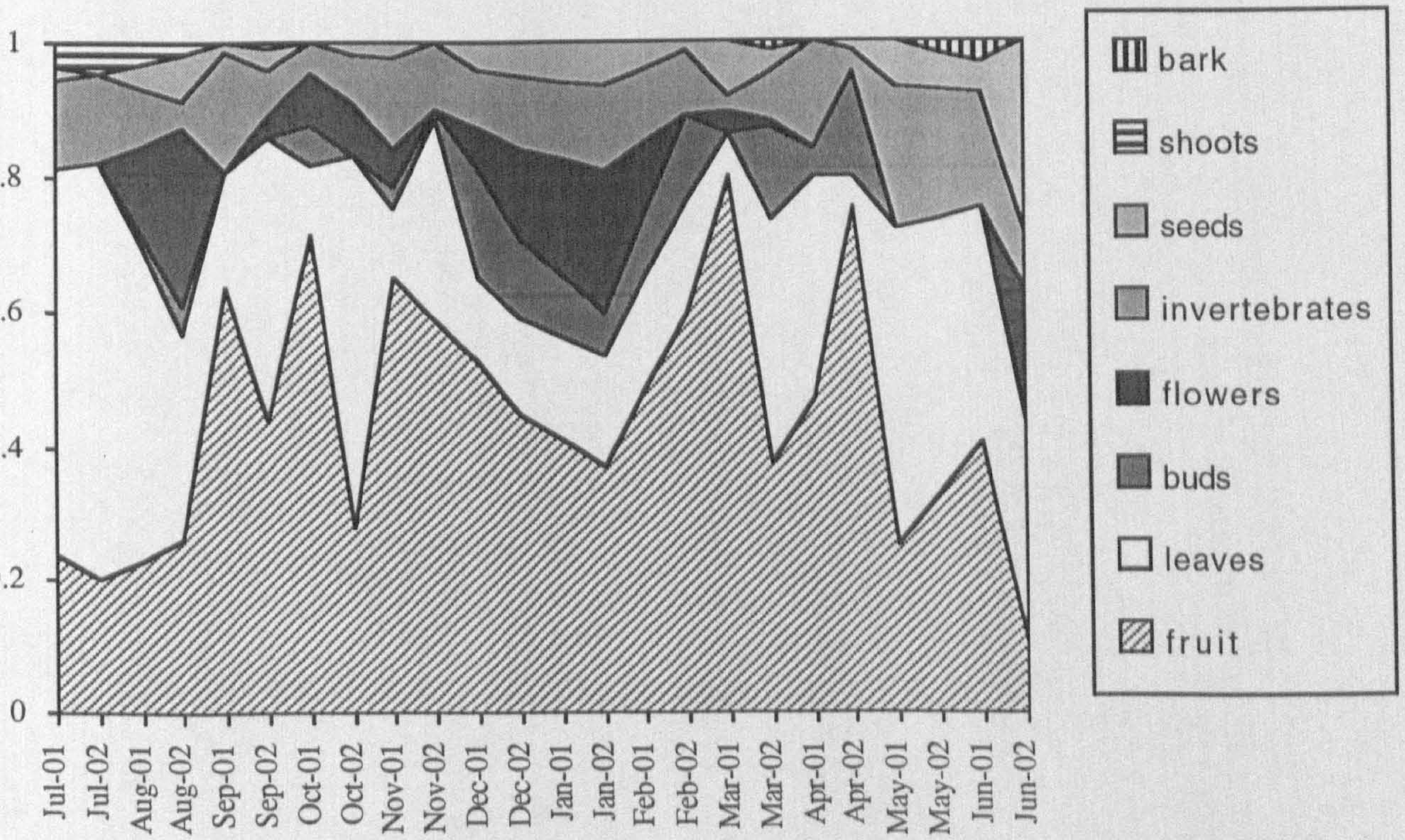


Figure 7.2.d. Group N152 Seasonal dietary composition

Seasonal Variation

Coefficients of variation (C.V.) were calculated for different food categories across all two day sample periods as an indication of annual variation in dietary composition (Table 7.3).

Table 7.3. Coefficients of variation for mean food category intake by bi-weekly sample period

Group	*Coefficient of Variation*				*n*
	Fruit	*Young leaves*	*Seeds*	*Invertebrates*	
N32	20.54	58.9	221.82	58.35	24
N31	34.63	57.89	160.18	65.64	21
N151	42.78	84.97	111.16	51.85	22
N152	42.08	61.56	144.59	50.79	19

Groups in N3 showed less variation in the proportion of fruit and the proportion of young leaves in the diet. Groups in N15 showed less variation in the proportion of invertebrates and the proportion of seeds. Variation in the intake of buds, flowers and shoots did not show any clear differences.

Dietary Overlap

Dietary overlap was calculated as the sum of the proportions of shared food items (Pielou 1966) for diet during 24 two week periods and compared between pairs of groups (Table 7.4). Ripe fruit/unripe fruit and mature leaves/young leaves were considered separately.

Table 7.4 Dietary overlap indices between groups in logged and unlogged forest. (No of shared items shown in brackets).

		Logged		*Unlogged*	
		N32	*N31*	*N151*	*N152*
Logged	*N32*	—			
	N31	0.870 (74)	—		
Unlogged	*N151*	0.570 (49)	0.650 (62)	—	
	N152	0.330 (49)	0.548 (60)	0.660 (66)	—

Dietary overlap indices show that the diet of groups within compartments (N3 and N15) shows a higher degree of overlap than diet between compartments (Table 7.4 - Logged: N31/N32 overlap = 0.870 and Unlogged: N151/N152 overlap = 0.660). Comparing individual pairs of groups, group N32 shows less overlap (0.570 and 0.330) with groups N151 and N152 compared to group N31 (0.650 and 0.548). The lowest degree of overlap occurred between group N32 and group N152.

Important Items In Overall Diet

In order to compare the important dietary items for the whole study period, the food items which accounted for the majority of feeding scores for each group were determined and compared between groups in N3 and N15. Feeding scores for invertebrates were excluded and items ranked by proportion of all feeding scores to give the top 20 items for each group (Tables 7.5.a and 7.5.b).

Table 7.5.a Top 20 plant food items by proportion of all feeding scores for groups in logged forest.

	Group N32			*Group N31*		
	Species	**item**	**p_i**	**Species**	**item**	**p_i**
1.	*Celtis durandii*	RF	0.191	*Cynometra alexandri*	YL	0.155
2.	*Cynometra alexandri*	YL	0.085	*Celtis durandii*	RF	0.121
3.	*Maesopsis eminii*	RF	0.083	*Maesopsis eminii*	RF	0.078
4.	*Ficus sur*	RF	0.069	*Celtis mildbraedii*	YL	0.074
5.	*Ficus sur*	UF	0.052	*Ficus lingua*	RF	0.066
6.	*Ficus exasperata*	RF	0.046	*Celtis zenkerii*	RF	0.055
7.	*Celtis mildbraedii*	YL	0.046	*Celtis durandii*	UF	0.032
8.	*Ficus exasperata*	UF	0.037	*Chrysophyllum albidum*	FL	0.018
9.	*Celtis durandii*	UF	0.031	*Cleistopholis patens*	RF	0.018
10.	*Ficus sansibarica*	RF	0.028	*Chrysophyllum albidum*	RF	0.017
11.	*Ficus sur*	BU	0.025	*Albizzia sp.*	FL	0.015
12.	*Maesopsis eminii*	UF	0.0218	*Morus lactea*	RF	0.015
13.	*Celtis zenkerii*	RF	0.021	*Cleistopholis patens*	RF	0.012
14.	*Albizzia sp.*	YL	0.016	*Croton macrostachyus*	RF	0.012
15.	*Khaya anthotheca*	BA	0.015	*Ficus exasperata*	UF	0.011
16.	*Alstonia boonei*	LP	0.012	*Alstonia boonei*	LP	0.011
17.	*Margaritaria discoidea*	RF	0.010	*Celtis zenkerii*	BU	0.010
18.	*Trilepsium madag.*	BU	0.010	*Maesopsis eminii*	UF	0.010
19.	*Cordia milleni*	UF	0.008	*Albizzia sp.*	YL	0.010
20.	*Ficus sur*	YL	0.008	*Albizzia sp.*	BA	0.010
Total			**0.8148**			**0.7500**

Table 7.5.b Top 20 plant food items by proportion of all feeding scores for groups in unlogged forest.

	Group N151 **Species**	**item**	**Pi**	*Group N152* **Species**	**item**	**Pi**
1.	*Maesopsis eminii*	RF	0.157	*Cynometra alexandri*	YL	0.158
2.	*Cynometra alexandri*	YL	0.156	*Celtis mildbraedii*	YL	0.115
3.	*Celtis mildbraedii*	YL	0.116	*Celtis zenkerii*	RF	0.059
4.	*Celtis durandii*	RF	0.107	*Ficus natalensis*	RF	0.055
5.	*Ficus lingua*	RF	0.064	*Ficus lingua*	RF	0.047
6.	*Cynometra alexandri*	FL	0.055	*Celtis durandii*	RF	0.047
7.	*Celtis zenkerii*	RF	0.049	*Maesopsis eminii*	RF	0.046
8.	*Chrysophyllum albidum*	RF	0.027	*Chrysophyllum albidum*	RF	0.045
9.	*Funtumia elastica*	SE	0.018	*Antiaris toxicaria*	RF	0.030
10.	*Cynometra alexandri*	SE	0.014	*Entandrophragma sp.*	SE	0.026
11.	*Morus lactea*	RF	0.014	*Teclea noblis*	RF	0.024
12.	*Celtis mildbraedii*	BU	0.013	*Alafia landolphioides*	RF	0.023
13.	*Celtis mildbraedii*	UF	0.013	*Celtis mildbraedii*	BU	0.023
14.	*Alafia landolphioides*	RF	0.010	*Cynometra alexandri*	FL	0.021
15.	*Holoptelea grandis*	BU	0.010	*Celtis mildbraedii*	UF	0.014
16.	*Celtis durandii*	UF	0.008	*Funtumia elastica*	SE	0.013
17.	*Mildbraedeodendron ex.*	RF	0.007	*Celtis zenkerii*	UF	0.012
18.	*Celtis zenkerii*	BU	0.007	*Celtis zenkerii*	BU	0.009
19.	*Alstonia boonei*	FL	0.007	*Trilepsium madag.*	UF	0.008
20.	*Celtis zenkerii*	UF	0.006	*Morus lactea*	UF	0.008
Total			**0.8580**			**0.7830**

The top 20 food items accounted for a similar percentage of all feeding scores in the four groups. Totals were 81.48 % and 75.00 % of all feeding scores for groups N32 and N31 respectively ; 85.80% and 78.30 % of all feeding scores for groups N151 and N152 respectively (Tables 7.5.a and 7.5.b). The frequency of different categories (ie. Ripe fruit, young leaves, buds etc..) in the top twenty items can be compared to assess which type of food items are important in the diet. Groups in N3 show a higher frequency of ripe and unripe fruit items in the top 20 dietary items while groups in N15 show a higher frequency of items in the 'other' category (Table 7.6). When the total proportion for each category is expressed as a percentage of the total for the top 20 items, then ripe fruit and unripe fruit accounts for a higher percentage of the top 20 items for group N32 and N31. This contrasts with groups N151 and N152 where 'other' items account for a higher percentage of the top 20 items in the diet (Table 7.6).

Table 7.6. Frequency of different food categories in the top 20 overall food items (Percentage of total shown in brackets)

	Ripe Fruit	Unripe Fruit	Young Lvs	Other *
N32	7 (54.97)	5 (18.40)	4 (19.02)	4 (7.61)
N31	9 (52.53)	3 (7.07)	3 (31.87)	5 (8.53)
N151	8 (50.70)	3 (3.15)	2 (31.70)	7 (14.45)
N152	9 (48.02)	4 (5.36)	2 (34.87)	8 (11.75)

* (Includes Buds, Flowers, Seeds and Leaf Petioles)

For groups in N3 (logged forest), the percentage of the diet which consists of ripe and unripe fruit is equal to or larger than the number of fruit items in the top 20. For N31 and N32, 12 fruit items out of 20 (60 %) account for 59.5 % and 73.37 % respectively of the total feeding scores. For groups N151 and N152, 11 (55%) and 13 (65%) fruit items respectively, account only for around 53% of the total feeding scores. For groups in N15, young leaves and 'other' items account for a high percentage of the diet relative to their frequency in the top 20.

Food Tree Abundance and Distribution

To compare the distribution and abundance of the top 20 food tree species, Coefficients of Dispersion and Importance Values were calculated for two groups (N32 and N151) using vegetation data and are shown below (Table 7.7). Species which were either very rare or very common were excluded from this analyses (indicated by n/a in Table 7.7).

Table 7.7. Importance values and Coefficients of Dispersion for top 10 plant food items by proportion of feeding scores: Group N32 (logged forest) and Group N151 (unlogged forest).

Group N32				*Group N151*			
Species	**Item**	**D**	**Imp.**	**Species**	**Item**	**D**	**Imp.**
1.*Celtis.durandii*	RF	n/a	24.92	1.*Maesopsis.eminii*	RF	0.82	4.50
2.*Cynometra.alexan.*	YL	0.85	17.00	2.*Cynometra.alexandri*	YL	n/a	78.68
3.*Maesopsis.eminii*	RF	1.56	8.86	3.*Celtis.mildbraedii*	YL	n/a	34.75
4.*Ficus.sur*	RF	3.08	13.75	4.*Celtis.durandii*	RF	2.75	7.59
5.*Ficus.sur*	UF	3.08	13.75	5.*Ficus.lingua*	RF	n/a	2.33
6.*Ficus.exasperata*	RF	3.00	4.39	6.*Cynometra.alexandri*	FL	n/a	78.68
7.*Celtis.mildbraedii*	YL	n/a	27.62	7.*Celtis.zenkerii*	RF	2.17	14.21
8.*Ficus.exasperata*	UF	3.00	4.39	8.*Chrysophyllum.albidum*	RF	1.03	5.25
9.*Celtis.durandii*	UF	n/a	24.91	9.*Futumia.elastica*	SE	2.65	11.31
10.*Ficus.sansibarica*	RF	n/a	2.36	10.*Cynometra.alexandri*	SE	n/a	78.68
11.*Ficus.sur*	BU	3.08	13.75	11.*Morus.lactea*	RF	1.13	1.51
12.*Maesopsis.eminii*	UF	1.56	8.86	12.*Celtis.mildbraedii*	BU	n/a	34.75
13.*Celtis.zenkerii*	RF	2.04	14.25	13.*Celtis.mildbraedii*	UF	n/a	34.75
14.*Albizzia.sp.*	YL	1.17	2.98	14.*Alafia..landolphioides*	RF	liana	n/a
15.*Khaya.anthotheca*	BA	4.45	14.73	15.*Holoptelea.grandis*	BU	0.83	1.89
16.*Alstonia.boonei*	LP	0.96	18.55	16.*Celtis.durandii*	UF	2.75	7.59
17.*Margaritaria.discoid.*	RF	1.27	8.16	17.*Mildbraedoed..ex.*	RF	0.93	1.31
18.*Trilepsium.madag.*	BU	0.99	4.62	18.*Celtis.zenkerii*	BU	2.17	14.21
19.*Cordia.milleni*	UF	1.27	6.34	19.*Alstonia.boonei*	FL	1.3	9.52
20.*Ficus.sur*	YL	3.08	13.75	20.*Celtis.zenkerii*	UF	2.17	14.21
Σ top 20 species			*247.94*				*435.72*

Testing for differences in the Coefficient of Dispersion and Importance Indices of the top 20 food items by Mann Whitney U test shows no significant difference (Dispersion: U= 133, P > 0.1; Importance: U=162, P > 0.1). When the Coefficient of Dispersion for trees producing only fruit items was compared, differences were still non-significant (U=29, P>0.05) but the median Coefficient of Dispersion and the sum of Coefficients of Dispersion are higher for trees in N3 (Table 7.8).

Table 7.8. Comparison of Coefficients of Dispersion (D) and Importance Values (IMP) for fruit and non-fruit items in the top 20 food items for 2 groups: N32= Logged forest; N151=Unlogged forest.

		Fruit items			*Other items* (YL, FL, BU, SE)		
		n	Median	Σ	n	Median	Σ
D	*N32*	9	2.04	19.86	7	1.17	14.58
	N151	8	1.65	13.75	4	1.3	6.95
IMP	*N32*	12	8.86	134.94	8	13.75	113.0
	N151	10	5.25	93.25	9	34.75	342.47

The food species featuring prominently in the diet therefore follow a similar distribution and abundance in the two ranges but the tree species whose fruit is important in the diet of group N32 have a much more clumped distribution in the range of group N32. Tree species whose fruit is important in the diet of group N151 have a less clumped distribution in the range of group N151. Summing the Importance values of tree species providing the top 20 food items (all items included), shows that tree species in the range of N151 have higher total Importance values than the equivalent species in the range of N32. If only the tree species producing ripe fruit and unripe fruit items are considered then N32 has a higher total. The tree species producing fruit items in logged forest are therefore more abundant, dominant and frequent in the vegetation.

Top five food items per 2 day sample

The proportion of the diet represented by the top 5 items in each two day period was similar in all four groups, the majority of the feeding scores being concentrated on a few species in most two day samples (Table 7.9). Groups in N15 (unlogged forest) had slightly higher median values for the proportion of the diet accounted for by the top 5 species suggesting that their main food intake was dervied from fewer items.

Table 7.9. Median proportion of diet accounted for by the top 5 items (n= No. of 2 day sample periods)

Group	*Median pi for Top 5 items*	*(n)*
N32	0.79	(23)
N31	0.81	(20)
N151	0.92	(22)
N152	0.82	(19)

As well as restricting the Selection Ratio calculations (see below) to the top five items, the frequency of occurrence of different items in each two day sample period can also be compared. These frequencies were expressed as a proportion of all top five food items (from 24 two-day samples). This gives an indication of type of items (i.e. fruits, leaves etc.) which are consistently important in the diet throughout the year (Table 7.10).

Table 7.10. Frequency of occurrence of different food categories in the top 5 items from all two day sample periods (Figures in italics indicate percentage of all top 5 items for that category).

		Category									
Group		*RF*	*UF*	*ML*	*YL*	*BU*	*FL*	*SH*	*BA*	*SE*	*Total*
N31	n	39	18	2	35	7	9	3	4	3	120
	pi	*0.325*	*0.150*	*0.016*	*0.291*	*0.058*	*0.075*	*0.025*	*0.033*	*0.025*	
N32	n	58	29	1	29	8	3	1	4	2	135
	pi	*0.430*	*0.242*	*0.007*	*0.242*	*0.059*	*0.022*	*0.007*	*0.030*	*0.014*	
N151	n	47	7	1	39	10	12	1	0	13	130
	pi	*0.361*	*0.054*	*0.007*	*0.3*	*0.077*	*0.092*	*0.007*	*0.00*	*0.100*	
N152	n	38	9	0	36	4	4	1	1	7	100
	pi	*0.380*	*0.090*	*0.00*	*0.360*	*0.040*	*0.040*	*0.010*	*0.010*	*0.070*	

As shown above, unripe fruit items were much more frequent in the top 5 items of groups in logged forest, while for groups in unlogged forest young leaves and seeds were more frequent. Bark items featured more frequently in the diet of groups in N3.

Selection ratios

Selection ratios were calculated for the top five food items eaten per two day sample by groups N32 (logged forest) and N151 (unlogged forest). The selection ratios for the top 5 items in each two-day sample are listed in Appendix 3. The ratio does not reflect true selection but gives an indication of the proportion of feeding scores for a particular item in relation to availability.

Comparing selection ratios for all of the top five food items using a Mann Whitney U test, group N32 (logged forest) shows significantly lower overall selection ratios for the top 5 food items throughout all sample periods ($U=4134$, $P<0.05$). Summing the selection ratios for the top five items in each two day sample shows much higher selection by group N151 in almost all sample periods (Figure 7.3).

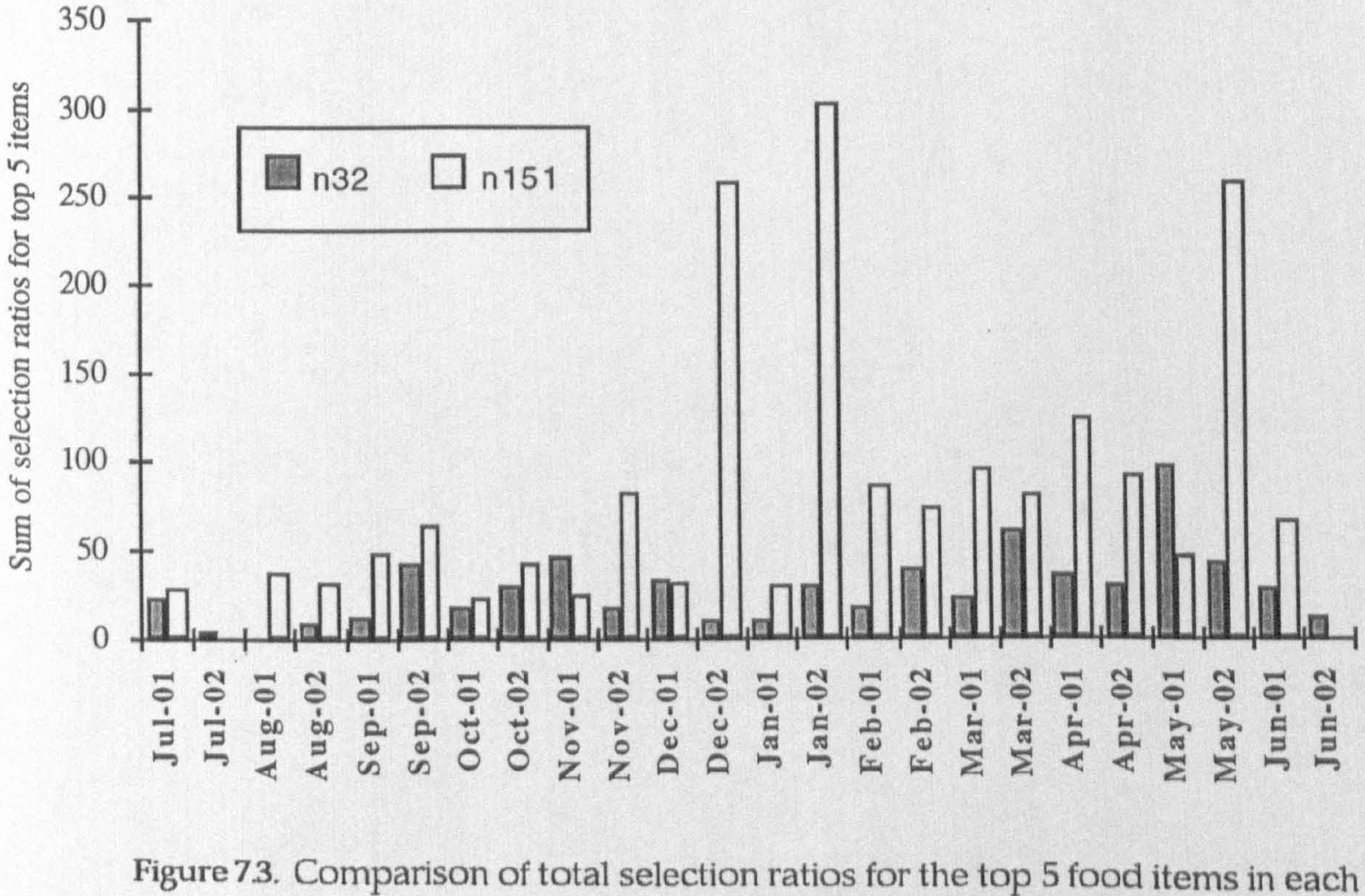


Figure 7.3. Comparison of total selection ratios for the top 5 food items in each two day sample: group N32 (logged) compared to Group N151 (unlogged forest)
(No data available for N32 - Aug. 1 and N151 - Jun 2)

During the dry seasons (Dec.-Feb. and May-Jun), selection ratios were much higher for group N151 due to a low food availability and a high frequency of feeding scores on very rare items. Group N151 selected most strongly for the following items:

Nov. 2:*Celtis zenkerii* ripe fruit, *Ficus spp* . young leaves
Dec. 2:*Trilepsium madagascarensis* ripe fruit, *Unidentified parasitic plant* ripe fruit.
Jan. 2:*Chrysophyllum albidum* ripe fruit , *Unidentified climber* buds
Feb. 1:*Chrysophyllum albidum* ripe fruit, *Alaphia landolphioides* (climber) ripe fruit.
Feb. 2:*Morus lactea* ripe fruit.
Mar. 1:*Maesopsis eminii* ripe fruit .
Apr. 1:*Iodes africana* (climber)ripe fruit, *Maesopsis eminii* ripe fruit
May 2:*Maesopsis eminii* ripe fruit , *Celtis mildbraedii* buds.

The only sample periods where group N32 shows stronger 'selection' for items in the top 5 compared to group N151 were May 1 and Nov 1 (for *Maesopsis eminii* ripe fruit and *Margaritaria discoidea* ripe fruit respectively). When selection ratios were compared by category (Mann-Whitney U test: ripe fruit, unripe fruit and young leaves), differences between N32 and N151 were only significant for ripe fruit items (Table 7.11). Therefore although able to maintain an intake of fruit in the diet, group N151 is apparently selecting more strongly for ripe fruit items in relation to their availability. This reflects the fact that groups N151 fed on rare items more frequently and fed on items of common species even when estimates of their abundance were low.

Table 7.11. Comparison between Selection Ratios (SR) for different food categories (all top five items from two day samples).

Category		*n*	*Median SR*	*U*	*Difference*
Young leaves	N32	23	0.72	311, ns	(N151>N32)
	N151	28	0.75		
Unripe fruit	N32	24	2.72	70, ns	(N32>N151)
	N151	7	2.15		
Ripe fruit	N32	51	4.93	398, $P<0.01$	(N151>N32)
	N151	43	17.73		
Buds	N32	7	1.56	11, ns	(N151>N32)
	N151	10	5.73		
Flowers	N32	3	3.59	25, ns	(N32>N151)
	N151	11	1.78		
Seeds	N32	2	14.21	n/a	
	N151	9	1.77		

There were also differences in the degree of selection between N32 and N151 for seeds, flowers (N32 selects more strongly) and buds (N151 selects more strongly) but these differences are not significant (Table 7.11).

Overall dietary diversity was similar for all four groups, N151 having the least diverse diet and N152 having the most diverse. Overall dietary evenness shows a similar pattern with no clear differences between logged and unlogged forest groups (Table 7.12).

Table 7.12. Overall dietary Diversity (H) and Evenness (E) in the four study groups

	Group	*H*	*E*
Logged	N32	3.19	0.68
	N31	3.34	0.67
Unlogged	N151	2.991	0.63
	N152	3.41	0.72

Dietary diversity was also calculated for each two day sample period (Table 7.13) using the Shannon Weiner index of diversity (ripe/unripe fruit and mature leaves/young leaves/buds considered separately).

Table 7.13. Dietary diversity and Evenness for two day sample periods (all groups)

	LOGGED				*UNLOGGED*			
GROUP	*N32*		*N31*		*N151*		*N152*	
	H	*E*	*H*	*E*	*H*	*E*	*H*	*E*
Jul. 1	2.64	0.88	1.71	0.71	1.54	0.70	–	–
Jul. 2	2.26	0.80	–	–	–	–	1.71	0.82
Aug. 1	–	–	1.84	0.80	1.73	0.75	–	–
Aug. 2	2.18	0.77	–	–	1.69	0.74	2.30	0.90
Sep 1	2.00	0.78	1.81	0.70	1.63	0.78	2.08	0.94
Sep 2	2.03	0.77	1.85	0.84	1.79	0.68	2.33	0.86
Oct. 1	1.75	0.65	1.70	0.61	1.68	0.81	1.87	0.78
Oct. 2	1.52	0.61	1.81	0.65	1.20	0.67	1.56	0.71
Nov 1	1.84	0.72	2.05	0.83	1.73	0.75	2.11	0.76
Nov 2	1.99	0.69	2.02	0.65	1.72	0.69	1.77	0.81
Dec. 1	2.11	0.72	1.80	0.70	1.75	0.68	2.09	0.75
Dec. 2	2.08	0.73	2.05	0.74	2.09	0.79	–	–
Jan. 1	2.39	0.88	–	–	2.34	0.89	–	–
Jan. 2	2.39	0.82	2.32	0.84	1.26	0.70	2.44	0.86
Feb. 1	1.70	0.82	1.67	0.73	2.40	0.80	2.35	0.85
Feb. 2	2.30	0.81	2.77	0.88	1.65	0.60	2.50	0.83
Mar 1	1.91	0.71	2.03	0.73	1.83	0.71	2.56	0.79
Mar 2	1.74	0.63	1.69	0.66	1.47	0.64	1.97	0.82
Apr 1	1.10	0.56	2.02	0.71	1.15	0.48	1.54	0.67
Apr 2	0.93	0.45	2.28	0.79	1.41	0.59	1.58	0.64
May 1	2.22	0.77	2.19	0.77	1.12	0.51	1.88	0.78
May 2	2.03	0.77	2.05	0.76	0.89	0.43	–	–
Jun 1	1.84	0.77	–	–	1.86	0.75	1.81	0.68
Jun 2	2.28	0.82	1.78	0.74	–	–	2.45	0.79
Median	**2.03**	**0.77**	**1.94**	**0.74**	**1.69**	**0.70**	**2.08**	**0.79**

All groups show some variation in dietary diversity indices as the proportion of different foods in the diet changes seasonally. Comparison of dietary diversity and evenness for two day sample periods showed significant variation (Kruskal Wallis $X^2=15.82$, $P<0.01$; $X^2=10.9$, $P<0.05$ for diversity and evenness respectively). Comparing pairs of groups by Mann Whitney U tests shows that group N151 has a significantly lower diversity index compared to all other groups (Table 7.13 and 7.14.a). Group N152 has a higher index of diversity compared to the other groups, but this difference is not significant. Differences in evenness are less distinct, the only significant difference between pairs of groups being that N151 has a less even diet compared to N152 ($U=90$, $P<0.01$, Table 7.15.b).

Table 7.14.a Mann Whitney U values testing for differences in dietary diversity between groups.

		Logged		Unlogged	
		N32	N31	N151	N152
Logged	N32	—	207 (ns)	121 (**)	199 (ns)
	N31		—	92 (**)	156 (ns)
Unlogged	N151			—	85 (**)
	N152				—

ns = P>0.05, * = P<0.05, ** = P<0.01.

Table 7.14.b Mann Whitney U values testing for differences in dietary Evenness between groups

		Logged		Unlogged	
		N32	N31	N151	N152
Logged	N32	—	226 (ns)	179 (ns)	147 (ns)
	N31		—	159 (ns)	121 (ns)
Unlogged	N151			—	90 (**)
	N152				—

ns = P>0.05, * = P<0.05, ** = P<0.01.

To investigate the influence of fruit intake on dietary diversity, Spearman rank correlation' coefficients were calculated between dietary diversity and proportion of fruit in the diet (Figures 7.4.a to 7.4.d). Dietary diversity shows a negative correlation with proportion of fruit in the diet for both logged forest groups (Figures 7.4.a and 7.4.b). Only group N32 shows a significant correlation (Spearman Rank correlation coefficient: R= -0.55, P<0.05) while N31 shows a negative but non significant correlation (Spearman Rank correlation coefficient: R= -0.31, P>0.1). Group N151 shows a weak negative correlation between proportion of fruit in the diet and dietary diversity while group N152 shows a very weak positive correlation (Figures 7.4.c and 7.4.d). Neither of these correlations is significant (Spearman Rank correlation coefficient: R=-0.21, P>0.1 and R=0.03, P>0.1 for N151 and N152 respectively). Dietary diversity is therefore influenced more by fruit intake in logged forest groups compared to unlogged forest groups. The relationships between dietary diversity and proportion of fruit in the diet reflects the fact that groups in N3 adjust their dietary diversity in relation to their intake of fruit. When fruit intake is high, their diet is likely to be less diverse and concentrating mainly on fruit items. When fruit intake is lower, the dietary diversity increases as other items are included. Groups in N15 show no clear relationship between fruit intake and dietary diversity.

LOGGED FOREST GROUPS

Figure 7.4.a. Group N32 (R= - 0.55: P <0.05)

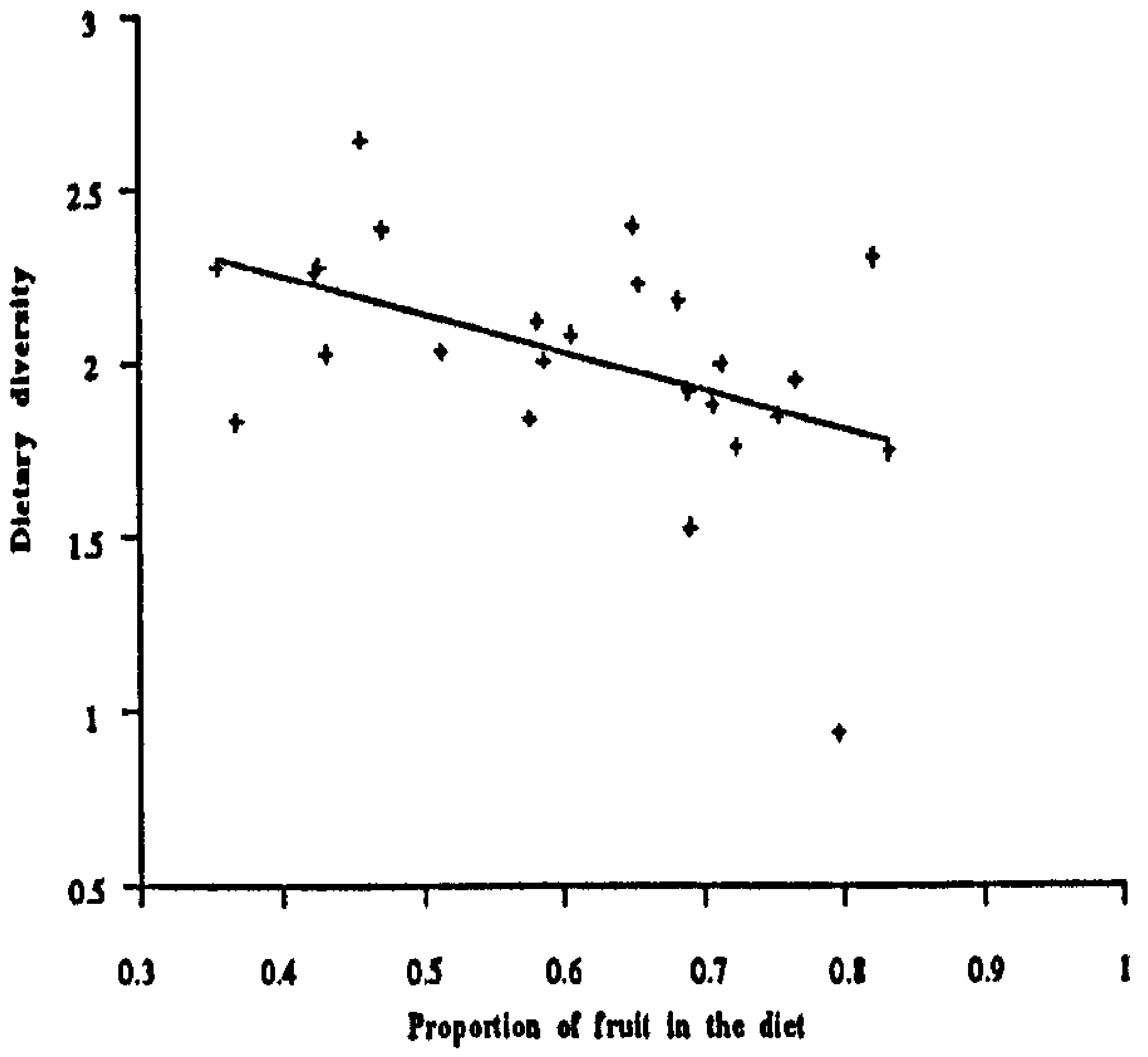
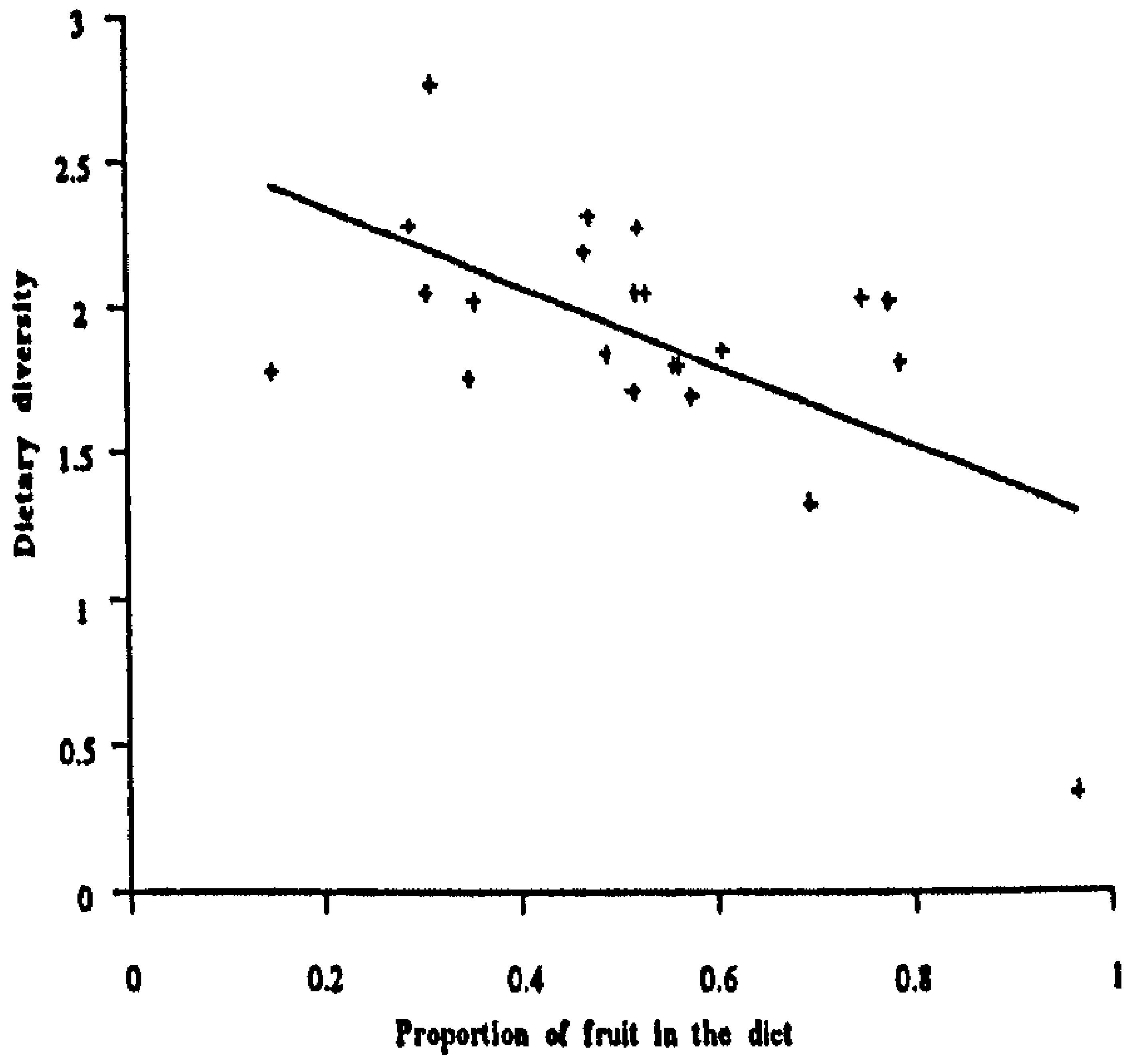


Figure 7.4.b. Group N31 (R= - 0.31: ns, P>0.1)



UNLOGGED FOREST GROUPS

Figure 7.4.c. Group N151 (R= - 0.21: ns, P>0.1

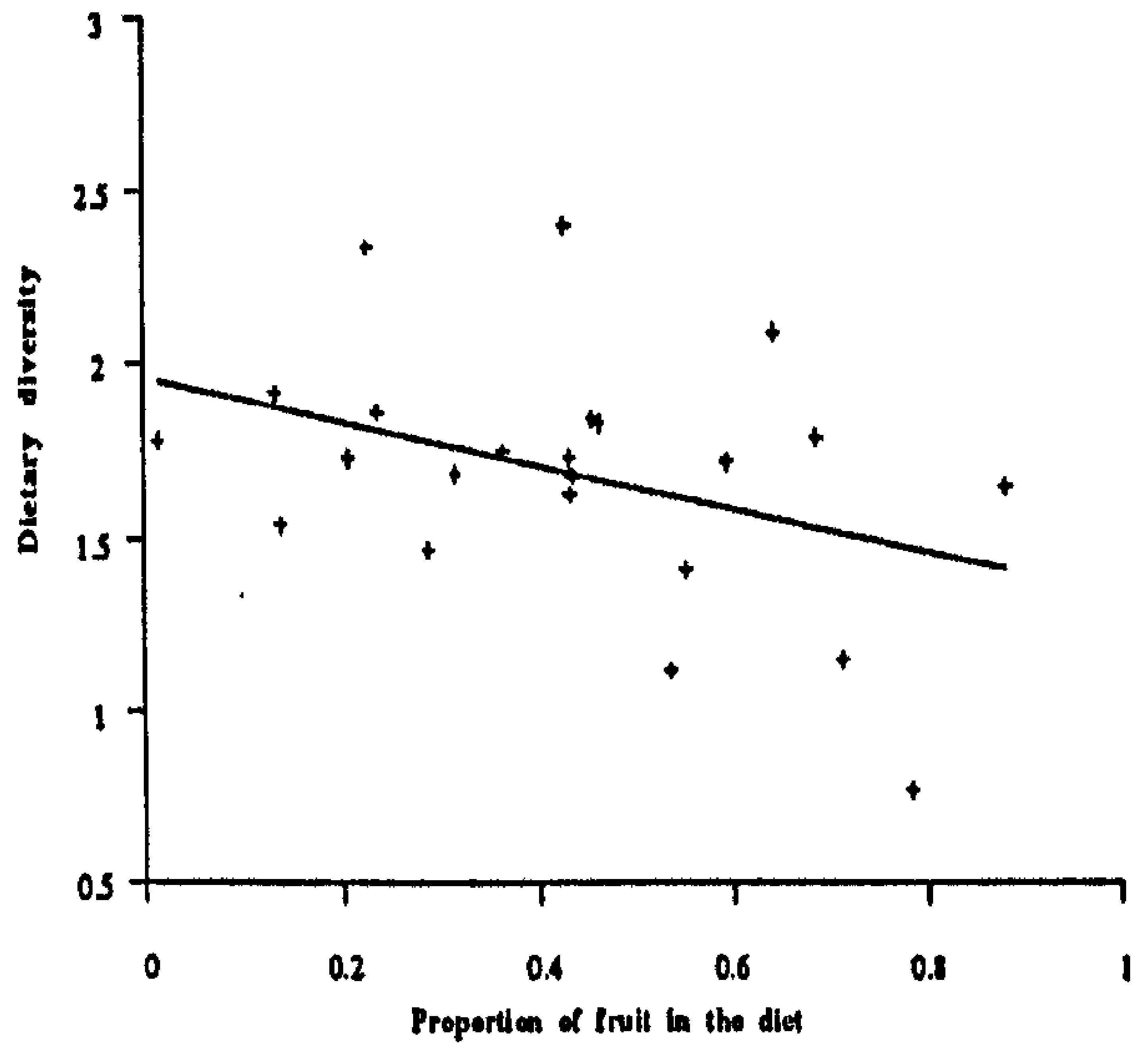
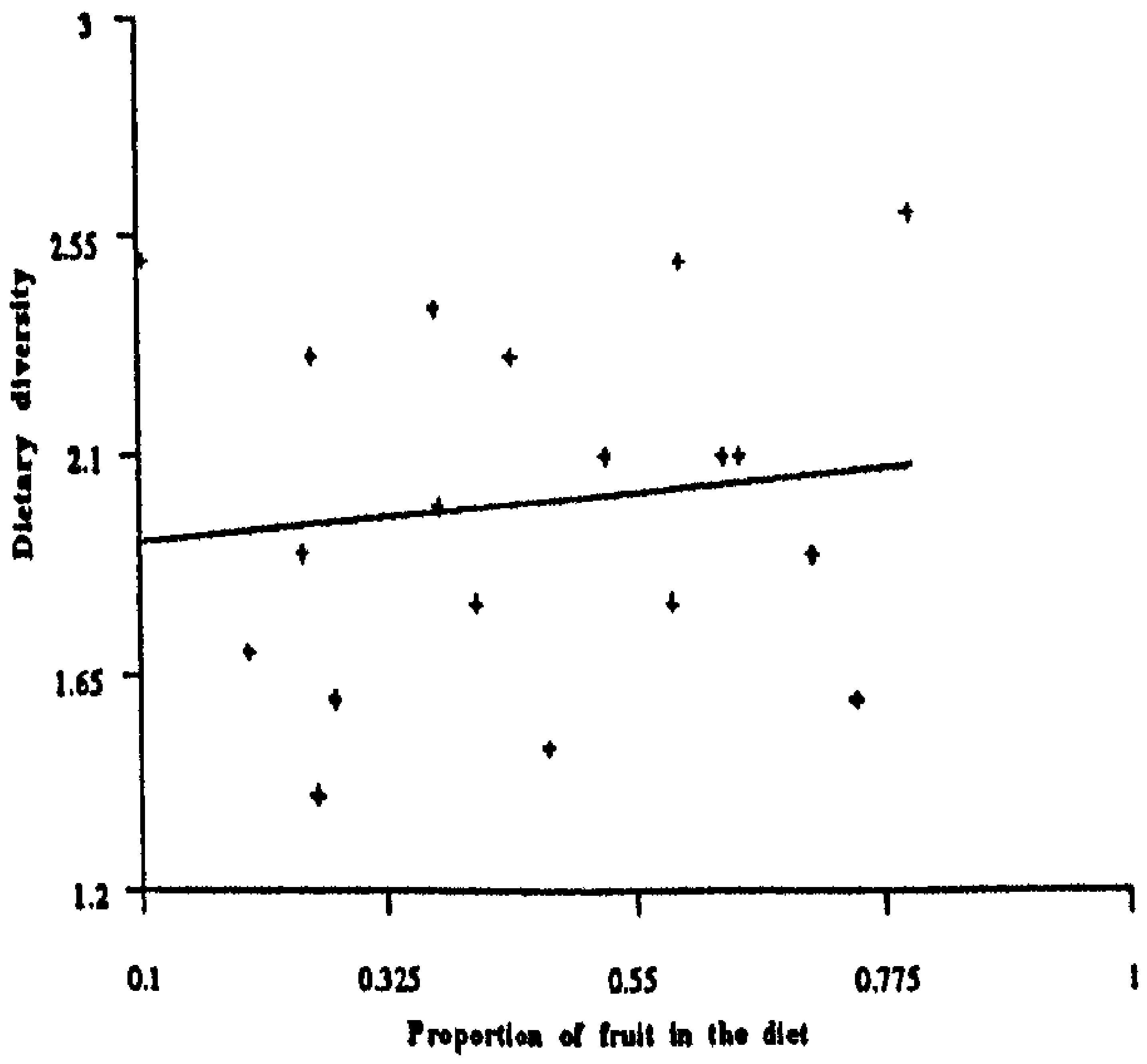


Figure 7.4.d. Group N152 (R=0.03: ns, P>0.1)



Figures 7.4 a to d Dietary diversity in relation to proportion of fruit in the diet for groups in logged (a.N32, b.N31) and unlogged (c. N151, d.N152) forest (Correlation coefficients and significance levels in brackets)

Dung Samples

A total of 206 faecal samples were collected from four groups during March 1993 to June 1994 of which almost 85% contained at least some intact seeds (table 7.15). A slightly higher percentage of all samples from Compartment N3 (logged forest) were found to contain at least some intact seeds due to the frequent occurrence of *Ficus* seeds in the dung of these groups.

Table 7.15. Number of dung samples collected containing intact seeds (% shown in brackets)

GROUP	*No. with seeds*	*(%)*	*No. without seeds*	*(%)*	*Total*
N3 (Logged)	118	(88.05)	16	(11.95)	134
N15 (Unlogged)	57	(79.16)	15	(20.84)	72
Total	175	(84.95)	31	(15.05)	206

Intact seeds were identified for a total of 12 tree species, 4 climbers and a further 8 unidentified species (table 7.16). Including all seeds, the mean number of seeds per sample was 69.5 (n=206, SD=118.10, Range=0-800). If seeds of several *Ficus spp.* are excluded from this calculation and only seeds > 2mm are included then the mean is considerably lower: Mean = 6.12 seeds per sample (n=147, SD=12.76, Range=0-92). The highest number of seeds > 2mm found in a single dung sample was 92 seeds of *Margaritaria discoidea* (2-3mm) and the largest seeds found intact in dung on several occasions were seeds of a climber, *Iodes africana* (up to 30 mm).

Table 7.16. List of seeds found intact in dung samples.

	Tree species	*n* *(% of all samples)**	*Mean No. of seeds per sample (Range)*		*Seed Size (mm)*
TREES					
	Ficus spp.	52 (25.2)	105.9	(2-400)	< 2
	Ficus sur	3 (1.45)	15	(5-20)	<2
	Ficus exasperata	23 (11.6)	157.2	(15-450)	<2
	Ficus lingua	15 (7.3)	247.5	(6-800)	<2
	Ficus sansibarica	2 (0.97)	5.5	(1-10)	<2
	All Ficus species	95 (46.11)			
	Margaritaria discoidea	47 (22.8)	10.8	(1-92)	2-3
	Morus lactea	15 (7.28)	25.5	(3-54)	4-6
	Celtis durandii	8 (3.88)	1.375	(1-2)	4-6
	Celtis zenkerii	21 (10.2)	5.19	(1-27)	6-8
	Maesopsis eminii	1 (0.48)	1†	(1)	13-15
	Myrianthus arboreus	1 (0.48)	1†	(1)	13-15
	Chrysophyllum albidum	2 (0.97)	1†	(1)	17-19
CLIMBERS					
	Maeso lanceolata	2 (0.97)	12	(3-21)	3-4
	Iodes africana	16 (7.77)	4.25	(1-9)	8-30
	Alafia landolphioides	10 (4.85)	1.5	(1-4)	19-22
	Piper guineense	1 (0.48)	1†	(1)	3-4
UNIDENTIFIED SPECIES					
	# 143	2 (0.97)	2.5	(2-3)	8-9
	# 36	3 (1.45)	8.33	(3-13)	4-5
	# 105	2 (0.97)	3	(1-5)	12-16
	# 130	2 (0.97)	6.5	(6-7)	1-2
	# 100	5 (2.43)	7.4	(1-16)	2-3
	# 149B	2 (1.41)	2	(1-3)	11-13
	# 158	2 (0.97)	1.5	(1-2)	8-16.5
	# 109A	2 (0.97)	1	(1)	1-12

† Denotes seeds which were normally observed to be processed and spat out from cheek pouches but may have been swallowed accidentally.

* NB Because some samples contained more than one species of seed the summed percentages are greater than 100.

As can be seen from Figure 7.5 , the most commonly found seeds (eg. *Ficus sp., Margaritaria discoidea*) were quite small in size. Some large seeds may have been swallowed accidentally as they were commonly observed being spat out of cheek pouches during follows (Table 7.17). However, large seeds which were seen being ingested (such as *Morus lactea, Celtis zenkerii, Iodes africana* and *Alafia landolphioides*) were also found intact regularly in dung samples.

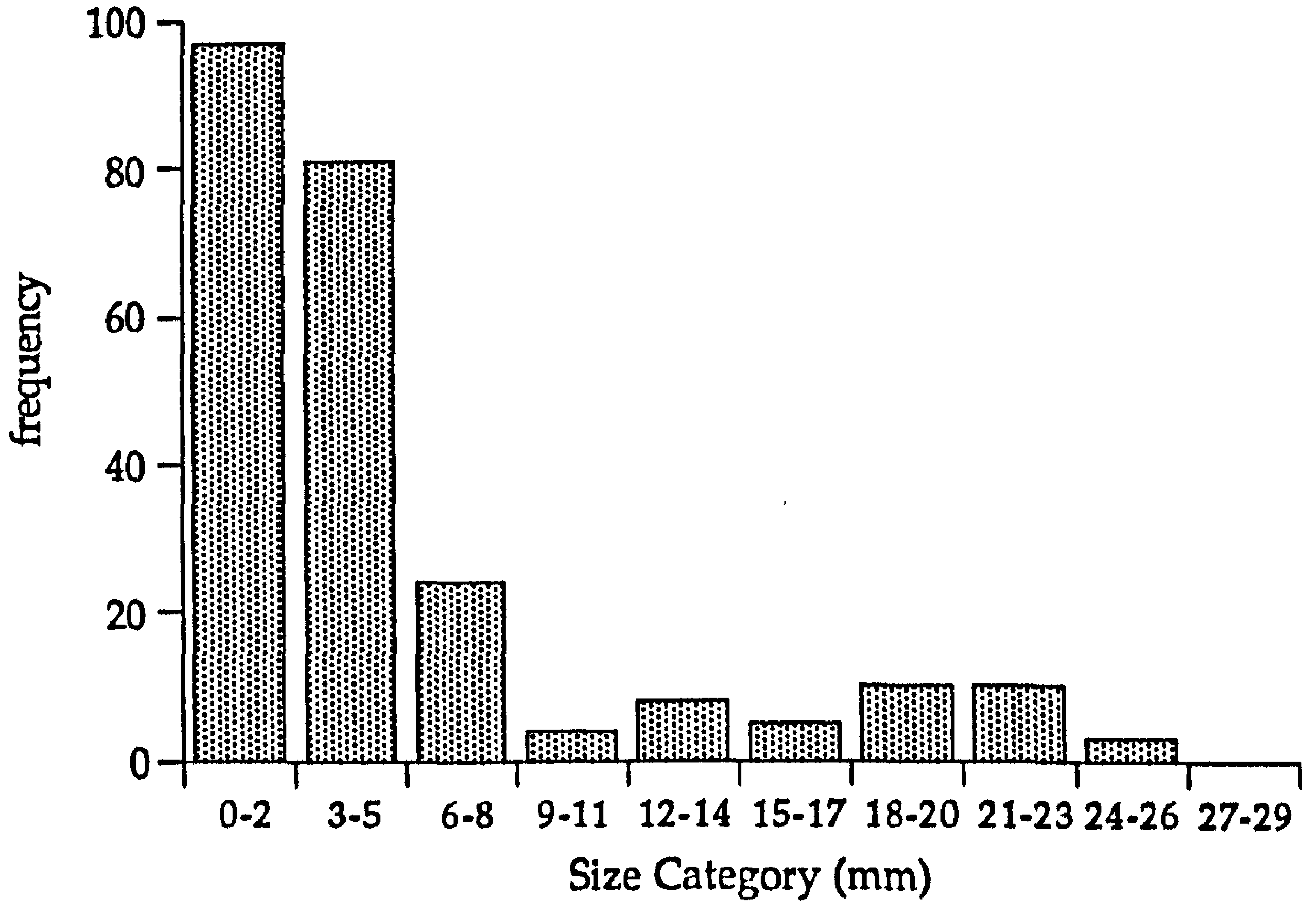


Figure 7.5. Frequency of intact seeds found in dung samples by 2mm size categories.

In addition to seeds found intact in dung samples, blue monkeys in Budongo may contribute to seed dispersal by spitting seeds from cheek pouches after cleaning the edible flesh off. Table 7.18 lists tree species where seeds were regularly observed to be spat from cheek pouches.

Table 7.17. Species with seeds regularly spat from cheek pouches by C.*mitis*.

Species	Seed size(mm)
Alafia landolphioides (Climber)	19-22
Antiaris toxicaria	5-10
Celtis zenkerii	6-8
Celtis durandii	4-6
Celtis mildbraedii	8-10
Chrysophyllum albidum	17-19
Cleistopholis patens	10-15
Coffea eugenoides	5-8
Cordia millenі	15-30
Iodes africana (Climber)	8-30
Maesopsis eminii	13-15
Mildbraedeodendron excelsum	10-20
Myrianthus arboreus	13-15
Teclea noblis	3-8

7.4 DISCUSSION

Overall Diet

A comparison of diet in different C.*mitis* populations where previously studied shows considerable differences in composition (Table 7.19). In all sites, fruit is the major component of the diet, supplemented by varying proportions of leaves, flowers, invertebrates and seeds. Blue monkeys in Budongo appear to have a high intake of fruit compared to other sites, supplemented by young leaves, invertebrates, flowers and seeds (in descending order of frequency). The relatively large body size of C.*mitis* amongst the guenons means that it is more likely to supplement its fruit intake with young leaves and other plant material than invertebrates (Gautier-Hion 1988). In Budongo, the proportion of invertebrates included in the overall diet is low compared to other studies (Table 7.19), and the flower, seed and fruit intakes are higher.

Table 7.18. Dietary composition in five populations of C.*mitis*

			% of total diet by feeding scores				
Species/study site		*Fruit*	*Leaf*	*Insect*	*Seed*	*Flower*	*Author*
C.*m.stuhlmanni* (blue monkey)							
Budongo Forest, Uganda	N3	55.8	21.8	8.55	1.45	4.55	1.
	N15	44.9	29.0	9.65	5.90	6.20	
Kibale Forest, Uganda	Ngogo	30.1	22.8	35.9	n/a	9.8	
	Kanyawara	25.5	28.9	40.3	n/a	5.35	2.
Kakamega, Kenya	54.6	18.9	16.8	3.0	3.6	3.	
Zomba, Malawi		24.2	51.9	0.3	n/a	17.9	4.
C.*m.eythrarchus* (samango)							
Cape Vidal, South Africa		51.7	25.8	5.8	n/a	13.4	5.

1. This study 2. Butynski (1990) 3.Cords (1987) 4.Beeson (1985) 5. Lawes (1991)

Dietary Differences Between Groups in Logged and Unlogged Forest

The most noticeable difference between groups in N3 and N15 is that groups in logged forest exhibit an increased unripe fruit intake (at the expense of young leaves and seeds), while groups in unlogged forest supplement their ripe fruit intake to a greater extent with young leaves, seeds and flowers. Nutritional requirements are met in guenons by combining carbohydrate and energy sources (fruit, nectar) with protein sources (invertebrates, young leaves and flowers). If protein requirements can be easily satisfied, then a higher intake of fruit may result in a nutritionally more rewarding diet. There is increasing evidence that fruit may be a limiting resource in guenons (Gautier Hion 1988, Lawes 1991), and competition for fruit a prime factor in causing dietary shifts. Therefore the higher fruit intake in N3 groups suggests that they are not limited by fruit and are less likely to show dietary shifts as a result of fruit shortages. Groups in N15 may be experiencing more limited fruit availability and consequently feed more on young leaves , seeds, and invertebrates during periods when fruit is not available. Kaplin (pers. comm.) reports that blue monkeys ranging in logged and unlogged forest in Nyungwe Forest, Rwanda, experience periods of fruit scarcity and at these times " became heavy seed predators... or they increased leaf consumption". Johns (1988a) reported an increase in leaf intake in some species following logging disturbance due to a reduction in available fruit but an increase in the proportion of trees bearing new leaves. This observation is contrary to this study but may have resulted due to the short interval since logging was carried out as well as the application of a higher logging intensity. Here I documented changes in dietary composition which are apparent almost 50 years after the logging event. Such dietary shifts have also been observed in natural forest systems where there is no disturbance due to logging. Gautier-Hion and Maisels (1994) documented extensive seasonal use of nectar (flowers) as a food resource, suggesting that this was an adaptation to cope with the seasonal shortage of fleshy fruits by guenons. Maisels and Gautier Hion (1994) concluded that where fruit is rare and Leguminoseae tree species abundant, monkeys increase their consumption of young leaves and seeds, mainly taken from Caesalpinoideae. This family is common in unlogged forest and species such as *Cynometra alexandri* (young leaves, flowers) and *Mildbraedeodendron excelsum* (seeds) provided food for groups N151 and N152 during times of fruit shortage. In addition, seeds of several Meliaceae (*Entandrophragma spp.*) were an important source of seeds. The two groups in N3, experiencing increased levels of energetically rewarding fruit in logged forest, may no longer have to undertake such extensive dietary shifts to maintain dietary quality.

Finally, it is interesting to note that both groups in N3 made more frequent use of bark (mainly *Khaya anthotheca* and *Albizzia spp*) and despite these tree species occurring in N15, their bark was rarely used as a food source by groups in N15. Consumption of bark has been recorded previously in other *C.mitis* populations (Beeson 1989, Maganga and Wright 1992) usually during periods of food shortage. In Budongo, feeding on *K.anthotheca* bark usually involved ingestion of the bark, while for *Albizzia spp.* the bark was licked and chewed before being discarded. The consumption of bark by groups in N3 was not confined to any particular period of the year and it has been suggested that the bark of *K.anthotheca* may have some medicinal properties (V. Reynolds pers.comm.). In addition, it may be that younger individuals of *K.anthotheca*, which are selected for bark feeding by *C.mitis* (per obs.) are more common in N3.

Dietary Differences and Effects on Population Density

It has been argued (Gartlan et al. 1980) that folivory may be a response to low levels of chemical defence making leaves a profitable food. If this is the case, then perhaps groups in N15 are still maintaining dietary quality via leaf intake. However, fruit is probably a preferred food item for *C.mitis* (Lawes 1991) and whenever available will be eaten in preference to young leaves, flowers and seeds. Lawes (1991) concluded that the high level of folivory in the *C.mitis* species group is of particular importance in relation to competition with congeneric species. By feeding on leaves, *C.mitis* can maintain an intake of easily assimilated protein. Lawes (1991) proposed several factors which could lead to a higher leaf intake: the absence of invertebrate sources of protein; a low tree species diversity; seasonality in fruit availability and competition. In those circumstances, he suggested that *C.mitis* is able to make use of leaves as a source of protein. The energetic costs of feeding on leaves however may be higher than simply increasing the intake of widely available fruit as groups in logged forest appear to be doing. Wrangham et al.(1993) found *Ficus spp.* to be an energy rich food with adequate protein also present. The difference in fruit intake between groups N32/N31 and N151/N152 is partly accounted for by a higher intake of 'fruits' of *Ficus spp*. The higher level of folivory and supplementary flowers, invertebrates and seeds in the diet of groups in N15 may indicate a lower dietary quality due to the lower tree species diversity and seasonal variation in fruit production (sensu Watermanet al 1988). Sommer and

Mendoza-Granados (1995) reported a high level of folivory in langurs (Presbytis entellus) and suggested that this was an indication of a poor quality habitat. Over a long term period, increasing the fruit component of the diet throughout the year may lead to an increase in female reproductive output and subsequent population increase (Milton 1982, 1993). Such changes would be relatively long term due to the low fecundity rate in most forest primates (Butynski 1990, Cords and Rowell 1987) but may be noticeable after a period of 45 years. It is also of interest to note that as discussed in Chapter 6, food availability may be higher during the birth and subsequent lactation period (Nov-March). Dunbar (1988) stated that up to 60% of a female primate's energy intake can be taken up by the infant during lactation therefore groups in unlogged forest may experience higher nutritional stress during this period as a result. If infant mortality were to be higher in unlogged forest due to the nutritional stress during lactation, then it would not be surprising to observe a higher birth rate in unlogged forest (see Chapter 4).

As well as the increase in dietary quality in logged forest, there may be less dietary overlap between blue monkeys and other species in N3 due to higher levels of food availability. Struhsaker (1978) observed that the degree of dietary overlap between blue monkeys and four other ecologically similar sympatric species in Kibale Forest was very high, and suggested that *C.mitis* was the primate species most likely to be affected by competition. By the same principle, he expected *C.mitis* would experience a high level of 'competitive release' in the absence of competitors. Gautier-Hion (1988) also suggest that the high degree of frugivory observed in Kakamega in *C.mitis* and *C.ascanius* is due to the absence of other species. Logging in Budongo may have the same effect as competitive release, i.e.. it results in a higher overall food availability and reduces inter specific competition, thus favouring an increase in *C.mitis* density. This may be important in determining the new population density in logged forest (Struhsaker 1978, Waser 1987).

Distribution and Abundance of Important Food Trees

Like most guenons (Gautier-Hion 1988) blue monkeys exhibit a diet where relatively few plant species make up the staple diet. In all four groups studied here, the top twenty food items by proportion of feeding scores constituted a high percentage of all feeding scores. If the changes in forest composition and food availability were to occur for any of the top 20 species in the diet as a result of logging then it is conceivable that such changes would have a significant effect on dietary quality. Comparing logged forest relative to unlogged forest, some changes in the abundance of important food trees is observed. Of the 15 tree species providing the top 20 items in group N32's diet, 11 species show an increase in abundance (relative to Importance values for unlogged forest). Of the four species showing a decrease in abundance (relative to Importance values for unlogged forest): *Celtis mildbraedii, Cynometra alexandri, Maesopsis eminii* and *Albizzia spp;* only one species produces fruit items featuring prominently in blue monkey diet and the other three produce young leaves and flowers which are included in the diet but are not 'important' items. This results in a significantly higher availability of fruit items which feature prominently and regularly in the diet of blue monkeys (see also Chapter 5 and 6).

Comparing the distribution of the tree species important in the overall diet, there are no differences in Coefficients of Dispersion or Importance Values when tree species producing items in all categories were considered together. The tree species producing the main dietary items therefore follow a similar pattern of distribution and abundance in logged and unlogged forest. However, when trees producing fruit items important in the diet and trees producing 'other' items important in the diet are considered separately, the tree species producing fruit items have a more clumped dispersion in N32 compared to N151. These tree species also have a higher sum of Importance values reflecting their high density, high frequency and dominance of basal area. Although not significantly different, the pattern is indicative of a more productive habitat in N3. This pattern of food tree distribution is also likely to affect the ranging patterns in N3, a suitable habitat with many fruit trees dispersed in a clumped pattern (see Chapter 8).

Top 5 dietary Items

Comparing the top 5 food items per 2 day sample period, ripe and unripe fruit items occur more frequently in the diet of groups in logged forest and represent a higher proportion of all items in the top 5 items. Comparison of these proportions confirms that the difference in fruit intake is mainly due to an increase in consumption of unripe fruit. Lawes (1991) also observed a high use of unripe fruit in C.*mitis erythrarchus* (16.2%) and attributed it to the low tree species diversity, small home range occupied and the low levels of plant chemical defence in unripe fruit. The level of species diversity is higher in Budongo, but as Lawes (1991) pointed out, while a species may be fruiting, ripe fruits may not always be available. Groups in N3 also occupy a smaller home range compared to N15 (Chapter 8) therefore may be forced to increase their intake of unripe fruit.

However, if unripe fruit is abundant, has low levels of chemical defence, and meets nutritional requirements, then dietary quality may be maintained and unripe fruit intake may be increased with no nutritional cost. The coefficients of variation for fruit intake in Budongo blue monkeys are higher (20-42: Mean = 35.00) than reported for samangos (17.9, Lawes 1991) and Kakamega blue monkeys (12.8, Cords 1986), but lower than those for blue monkeys at other sites (42.8-77.3, Lawes 1991) suggesting that fruit is less limiting in Budongo. It is also important to point out that ripe fruit intake in logged forest groups is still maintained even when unripe fruit intake is high, therefore the high intake of unripe fruit is an additional intake, and does not act as a substitute for ripe fruit.

Seasonal diet

There are no real differences in the seasonal patterns of dietary composition between logged and unlogged forest, all four groups showing some degree of seasonal variation. Seasonal intake of fruit is more constant in N3 compared to N15 as indicated by the lower coefficient of variation in fruit intake for groups N31 and N32. A high variation in fruit intake may be indicative of the fact that fruit is a more limiting resource (Lawes 1991) therefore fruit may be more limiting in N15. By contrast, the coefficients of variation for seeds and invertebrates are lower for groups in N15 reflecting a more constant intake of these categories of food.

Selection Ratios

Estimates of 'selection' of different items by two of the groups (N32 and N151) were made and differed greatly between the two areas. Previous studies have estimated selection (Rudran 1978, Harrison 1984), but do not take seasonal patterns into account. Selection ratios may vary seasonally, especially during periods of food shortage. Here I attempted to investigate seasonal changes in the way items were fed on in relation to their availability. Group N151 (unlogged forest) showed a higher degree of selection for the top 5 food items throughout the 12 month study period. In other words, they more frequently fed on items which were rare or had low availability estimates. In addition group N151 showed a significantly higher degree of selection for ripe fruit items compared to group N32 (logged forest). This observation together with the fact that groups in N15 eat a much lower proportion of unripe fruit suggests that fruit is more limited in unlogged forest and preference is for ripe fruit among blue monkeys groups there - eating ripe fruit may provide higher levels of nutrition. There is also an observed increase in the degree of 'selection' during the long dry season by group N151 reflecting the scarcity of fruit in their range at this time of year and the high frequency of feeding on the fruit or young leaves of rare trees and climbers. The limited availability of food at certain times of the year will have important consequences for dietary quality and may be important in determining carrying capacity of the habitat (Cant 1980, Terborgh 1986). There may therefore be more 'ecological stress' on groups in unlogged forest during the dry season period of food shortage.

Dietary Diversity and Evenness

Overall dietary diversity and evenness do not differ significantly between logged and unlogged forest groups. The exception is group N151 which shows a lower dietary diversity than group N152 and a less even diet than all of the other groups. This probably reflects the fact that dietary differences are in terms of food categories rather than the number and relative proportions of different items. However, dietary diversity is inversely correlated with fruit intake for both groups in N3 (logged forest), but shows no clear relationship with fruit intake for both groups in N15 (unlogged forest). This reflects the strong influence of fruit intake on the inclusion of other items in the diet in logged forest. Both groups in N15 show a very weak negative or a weak positive correlation (both non-significant) indicating that the level of fruit in the diet does not determine the intake of other items. Fruit therefore would appear to be the preferred food of groups in logged forest and plays an important role in determining overall dietary composition. By contrast in unlogged forest, probably due to a lower level of fruit availability, dietary diversity is not related to fruit intake and thus fruit plays a less important role in determining dietary composition.

Seed Dispersal: The Role of Blue monkeys as Dispersal Agents

Analysis of dung samples shows a range of seeds from several tree and climber species being passed intact in the dung. Although many of these seeds were small (< 2mm), samples were frequently found to contain relatively large seeds sometimes in large numbers. This suggests that, for some trees and climbers, blue monkeys in Budongo may play at least some role in the first stages of seed dispersal.

The findings of the few previous studies of the role of blue monkeys as dispersal agents have been somewhat contradictory. Rowell and Mitchell (1991) in their study in Kakamega classified blue monkeys as seed destroyers and concluded that "it seems unlikely that faecal deposition contributes to seed dispersal". Wrangham et al. (1994) described blue monkeys as dispersers but of limited importance relative to chimpanzees in Kibale Forest, Uganda. Recent results from a study of blue monkeys in Nyungwe (B.Kaplin pers.comm.) documented seeds of 17 species intact in the dung (trees: 7 spp., understorey shrubs: 5 spp., and climbers: 5 spp.) . These seeds ranged in size from 0.5 - 13.25 mm in size (mean=3.91 mm). As observed during this study, it was found that the frequency of intact seeds in the dung varies seasonally, according to fruit intake. Kaplin concludes that "during certain periods of the year, the monkeys are seed dispersers, during other times seed predators....depending on forest tree phenology and diet composition" (B.Kaplin, pers. comm.).

Several points should be noted regarding the Kakamega and Kibale data. Firstly, that fewer seeds were found in the dung samples could be due to the short time period over which very few samples were collected. Wrangham's (1994) estimate of 0.37 seeds per sample was for three arboreal monkey species (n=84) of which blues constituted only 20 samples. Rowell and Mitchell (1991) also collected an unspecified number of samples over a very short period of three months. By contrast, this study involved collection of a much larger sample (n=206) over a 16 month period. It is likely that the seed content of dung samples varies considerably, largely determined by seasonal patterns of food production and fruit intake. A longer term with a larger number of faecal samples collected, will give a better indication of the true frequency of seeds in dung.

There may also be differences in the extent to which blue monkeys are dispersing seeds relative to the amount of fruit they include in the diet. As shown above (Table 7.19), blue monkeys in Budongo exhibit a relatively high degree of frugivory compared to Kibale and Kakamega and this may lead to a high number of seeds being passed intact in the dung. The seed treatment with regard to specific fruits is probably determined by the size of the seed and the nature of the pulp attachment. From the results of this study and another involving long term collection of samples (Kaplin pers. comm.), it would appear that blue monkeys have a definite role as seed dispersal agents even if this role is limited to certain tree species and seed types.

Conclusions

i) Overall dietary composition for all four groups was similar to the diet reported from previous studies of *C.mitis* but all four groups in this study appear to have relatively high intake of fruit.

ii) Comparing the two compartments, groups in logged forest have a higher, more constant intake of fruit in their diet compared to groups in unlogged forest. Groups in unlogged forest supplement their fruit intake to a much greater extent with invertabrates, leaves and seeds.

iii)These differences in diet reflect the differences in habitat composition and resource distribution (spatial and temporal) which occur as a result of vegetation changes associated with logging. It is also highly likely that the differences in dietary composition are important in terms of dietary quality and nutrition: groups in logged forest having a better quality diet.

iv) Blue monkeys in Budongo, as in one other previous study (Kaplin pers. comm.), appear to pass intact seeds of several tree and climber species therefore may play a greater role as seed dispersal agents than previously thought (Rowell and Mitchell 1991).

CHAPTER 8

ACTIVITY AND RANGING PATTERNS

8.1 INTRODUCTION

There is considerable agreement that range size and ranging patterns in primates are largely determined by food availability and distribution (Gautier-Hion 1988, Harrison 1984, Newton 1992, Rodman 1978). Based on the differences in vegetation composition and food availability between logged and unlogged forest (Chapter 5 and 6), it is expected that range size, range use and activity patterns will differ between logged and unlogged forest. Use of range and activity patterns will also reflect the adoption of different foraging strategies (Garber 1987). Such differences may be important in determining the carrying capacity of logged and unlogged forest. Johns (1986) stated that "changes in ranging patterns occurring as a result of logging will, to a certain extent, be consistent with changes in the cost efficiency of certain food items". He documented changes in proportion of time spent feeding, resting and travelling following logging. A study of *C.mitis erythrarchus* , a member of the *C.mitis* group at the extent of its range, showed activity patterns divergent from other *C.mitis* in seasonal and diurnal timing of activities (Lawes and Piper 1992). Activity patterns are influenced by body size, metabolic requirements, costs of thermo-regulation as well as nutritional quality and quantity of food (Dunbar 1988, Lawes and Piper 1992, Sommer and Mendoza-Granados 1995). Of these factors, only food quality and quantity would be likely to vary between neighbouring groups in Budongo although as discussed in Chapter 7, costs of lactation etc. may differ slightly. Therefore one would predict differences in activity patterns mainly as a result of variation in food quality and quantity.

In addition to differences in activity patterns, differences might be expected in overall size and patterns of use of home range areas between N3 and N15. Food availability and group energetic requirements are important in determining the total size of range in female-bonded primate groups (Wrangham 1980). Differences in habitat-wide food availability between logged and unlogged forest may result in different sizes of home range. There is evidence that the distribution of food trees is important for determining ranging patterns in cercopithecids (Freeland 1980, Garber 1987, Harrison 1983). As well as the spatial distribution, temporal availability of food resources plays an important part in determining patterns of range use. Changes in the distribution and abundance of tree species is commonly associated with disturbance due to logging (this study, Cannon et al 1994, Hall unpubl., White 1994a), and therefore changes in ranging patterns would be expected between logged and unlogged forest (Johns 1983, 1985c).

Techniques used in estimating home range size are important in determining the accuracy of both area estimates and patterns of range use (Kool and Croft 1992, Olson 1986). Most parametric techniques require data points to be independent and where this assumption is not met (as in this study) then non-parametric techniques must be used (Worton 1987).

8.2 METHODS

Activity Patterns

As with feeding scores, activity scores were corrected for age-sex class sampling bias (see Chapter 6). For each age-sex class, uncorrected activity scores were divided by the total number of activity scores for that age-sex class to give an uncorrected proportion. This uncorrected proportion was then multiplied by the expected number of activity scores for the age-sex class to give a corrected score for that age-sex class for that activity category. Corrected scores for each age-sex class were then summed and proportions for activity categories were calculated for each group.

Corrected proportions were then compared over i) the 12 month study period (24 two week periods and ii) each bi-weekly sample period. Proportions were calculated for the following categories:

Feeding/Foraging
Moving
Resting
Social : all forms of grooming, playing etc. combined
Vigilance/vocalisation: includes territorial calling and inter-group interactions.

These categories combine some of the original categories (See Chapter 3) and were used throughout the analyses.

Home Range Estimates and Ranging Patterns

Movements of all four groups during dawn to dusk follows were plotted on 1:3000 scale maps of the appropriate area of trail grid system (Chapter 3). Co-ordinates of location points were later recorded from the maps using acetate overlay grids. The acetate overlays consisted of a 10m grid of cells laid out on x and y axes and co-ordinates for each location point were read off using the grid cells. Location points were not independent but were collected over a sufficiently long period of time to allow non-parametric analyses using Wildtrak to be carried out (Todd 1993). Only follows which resulted in >20 location records (5hrs) were included in the analyses.

Three types of analysis were carried out to give estimates of home range size and use: i)Restricted polygon analysis, ii) grid cell analysis and iii) grid cells analysis with peripheral influence (Todd 1993):

i)Restricted polygon analyses.

Analyses known as 'polygon analyses', involve connecting the outer limit location points in a range using a straight line and calculating the area enclosed by the resulting polygon. Two types of polygon analyses are commonly used. The first of these, minimum convex polygon analyses, includes all data points and can lead to outlying points contributing disproportionately to the shape of the range. This can result in an overestimate of home range size, especially where home ranges are small (Kool and Croft 1992). Restricted polygon analysis however, uses a similar method but excludes outlying points which would contribute disproportionately to range size. This is achieved by setting the condition that no side of the polygon may be longer than the arithmetic mean distance of all the points from the centre of the range (Todd 1993). Since the analyses carried out here were designed to give a comparable estimate of range size in relatively small home range areas, restricted polygon analyses were therefore considered more appropriate for estimating total range size.

ii) Grid Cell Analyses.

This method gives an indication of the total number of grid cells entered-hence a more accurate estimate of the total area actually used. It also gives an indication of the intensity of use of different cells. To carry out grid cell analyses, a grid cell size of 20 x 20 m was selected. This gives a reasonably fine 'grain' of cell (Olson 1986) which would probably include the majority of the individuals in the group (original location plots were for the 'estimated centre of mass' for the individuals sampled during the scan). Olson (1986), discusses the importance of selecting an appropriate grid cell size and concludes that in addition a 'floating' rather than a 'fixed' grid will provide a more accurate estimate of home range. If a fixed grid is to be used, the grid cell size should be of the smallest size possible. The cumulative number of grid cells (expressed as % of total range) was also calculated and plotted against number of fixes to investigate the rate of accumulation of grid cells (range area) throughout the study period.

iii) Peripheral Influence Grid Cell Analyses

To give a smoothed representation of the home range, an estimate was made using Peripheral Influence grid cell analyses. For this analysis a grid cell size of 20 x 20m was used and all cells occupied were assigned with a score of one. In addition, each of the 8 cells surrounding an occupied cell were assigned a value of 1/8. It is likely that all individuals in a group were dispersed over a larger area than the 20m grid cell where the estimated centre of mass (for the individuals which were included in scans) was recorded. This estimate may therefore give a more appropriate estimate of range size and use for the whole group. In addition, it gives a smoother representation of range, filling in the 'holes' in the central parts of the range.

Range overlap

Overlap in temporal use of home range was calculated using Wildtrak as i) the range (hectares) used in two consecutive two-day sample periods and ii) the percentage of the previous sample's range used in any sample period.

Daily path length and Defendability

Daily path length was calculated for all days with more than 5 hours contact with groups (20 location points). Wildtrak calculates the daily path length as the summed straight line distances between consecutive fixes from the beginning to the end of the diurnal activity. This will probably be a minimum estimate of the actual movement of the group, but is comparable between groups in logged and unlogged forest. Using the mean daily path length and home range area estimated by the restricted polygon technique , the index of defendability (D) was calculated for each of the four groups (Mitani and Rodman 1979). This index is calculated as the mean daily path length (d) divided by the diameter of a circle (d') with an area equivalent to the total home range. The potential for frequent contacts with range boundaries (range defence) is implied when D is high while a low value of D implies infrequent contact (defence is difficult). In addition, Wildtrak calculates the percentage of all fixes where a change in group location had occurred, which gives an estimate of the proportion of all contact hours where groups were moving.

Canopy Use

To examine vertical use of range, canopy layer use was compared by proportion of scans where individuals were recorded at different canopy heights. A ratio was then calculated to investigate canopy layer use in relation to estimated canopy cover at different heights.

8.3 RESULTS

Comparison of the proportion of all scores in different activity categories for the twelve month period did not show any differences in activity budgets (Table 8.1 and Figures 8.1.a to 8.1.d). All groups spent the majority of their time during follows foraging or feeding. The remaining time was divided between social activity (playing, grooming etc.), resting, moving, and vigilance/vocalising (in descending order of importance: Figures 8.1.a to 8.1.d). The proportion of scores in different categories was compared using data from two-day sample periods by Kruskal Wallis analysis of variance. There was no significant variation between groups for any of the activity categories (see Table 8.1 for X^2 values). Group N152 shows the highest proportion of time spent feeding/foraging while group N32 spends the most time moving. Although there were no differences in the proportion of time spent feeding/foraging or moving, both groups in unlogged forest did show a lower proportion of time resting.

Table 8.1. Proportion of scores in different activity categories for four groups.

	Logged		*Unlogged*			
	N32	*N31*	*N151*	*N152*	X^2	
Feeding/Foraging	0.489	0.500	0.498	0.541	5.67	ns
Movement	0.130	0.101	0.113	0.107	4.6	ns
Social	0.176	0.162	0.184	0.154	2.15	ns
Resting	0.146	0.148	0.141	0.138	1.66	ns
Vigilance/Vocalising	0.058	0.088	0.064	0.060	5.87	ns

ns = not significant, * = P<0.05, ** = P<0.01, *** = P<0.001

N3:LOGGED FOREST

Figure 8.1.a.

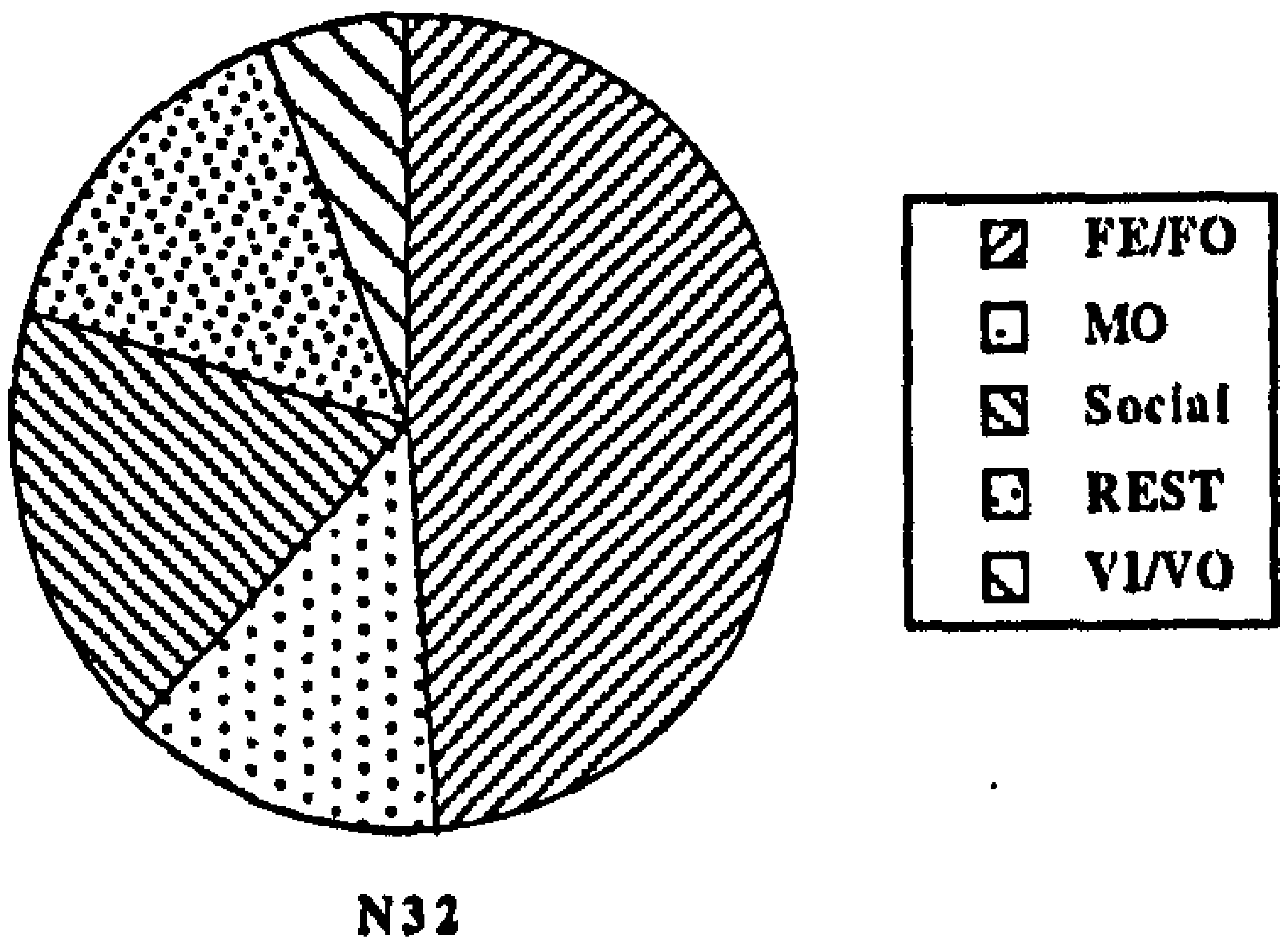
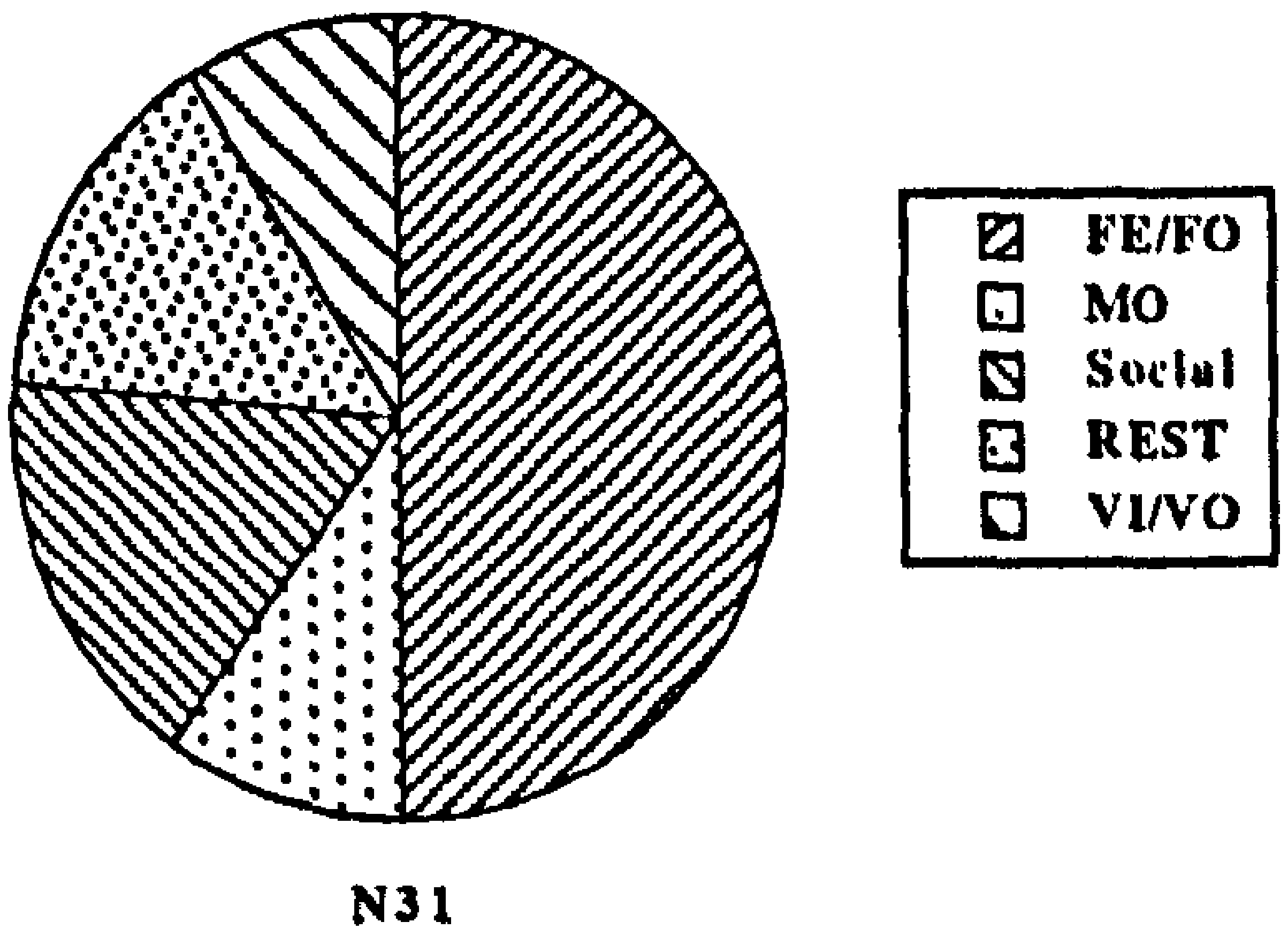


Figure 8.1.b.



N15:UNLOGGED FOREST

Figure 8.1.c.

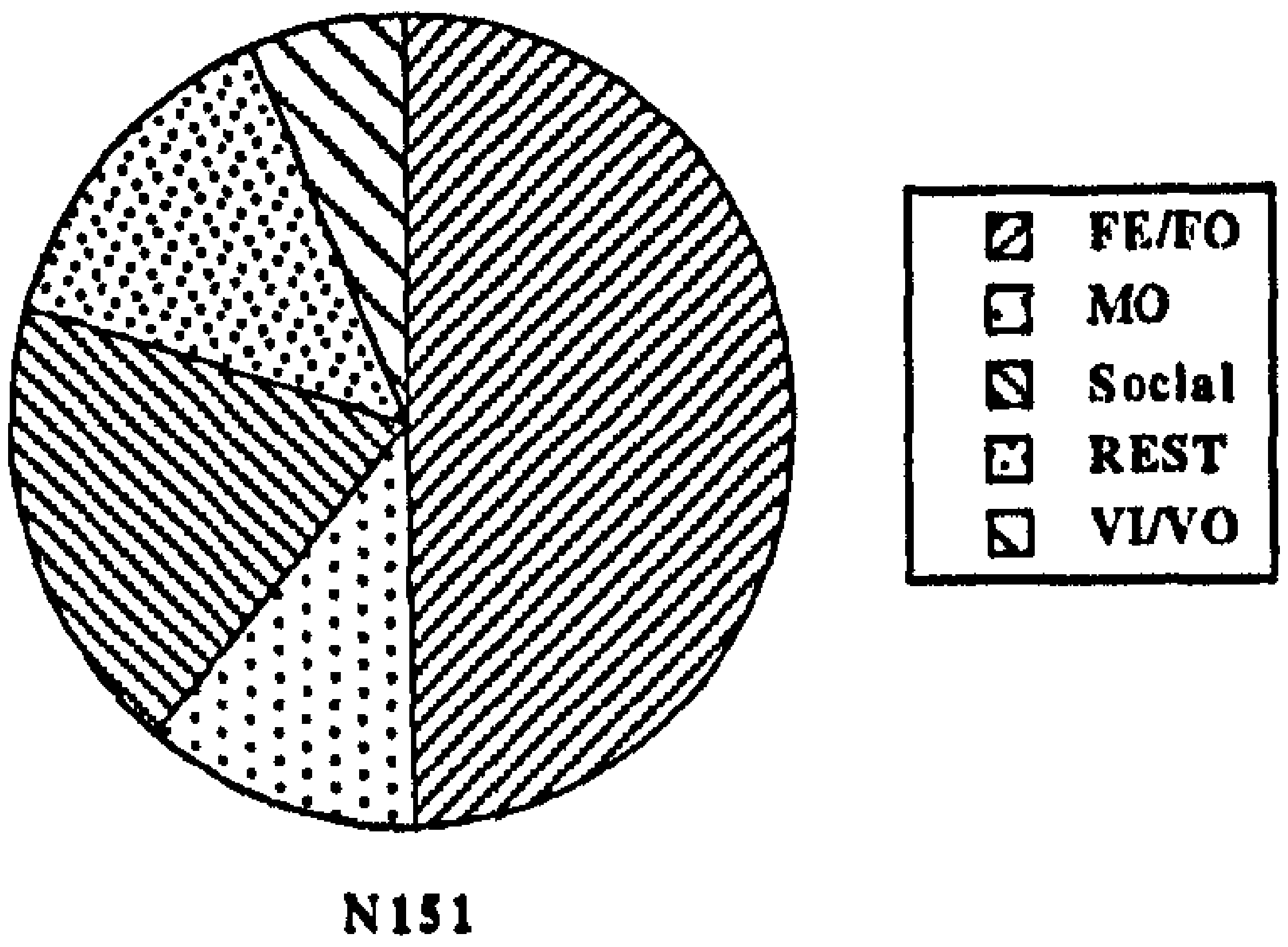
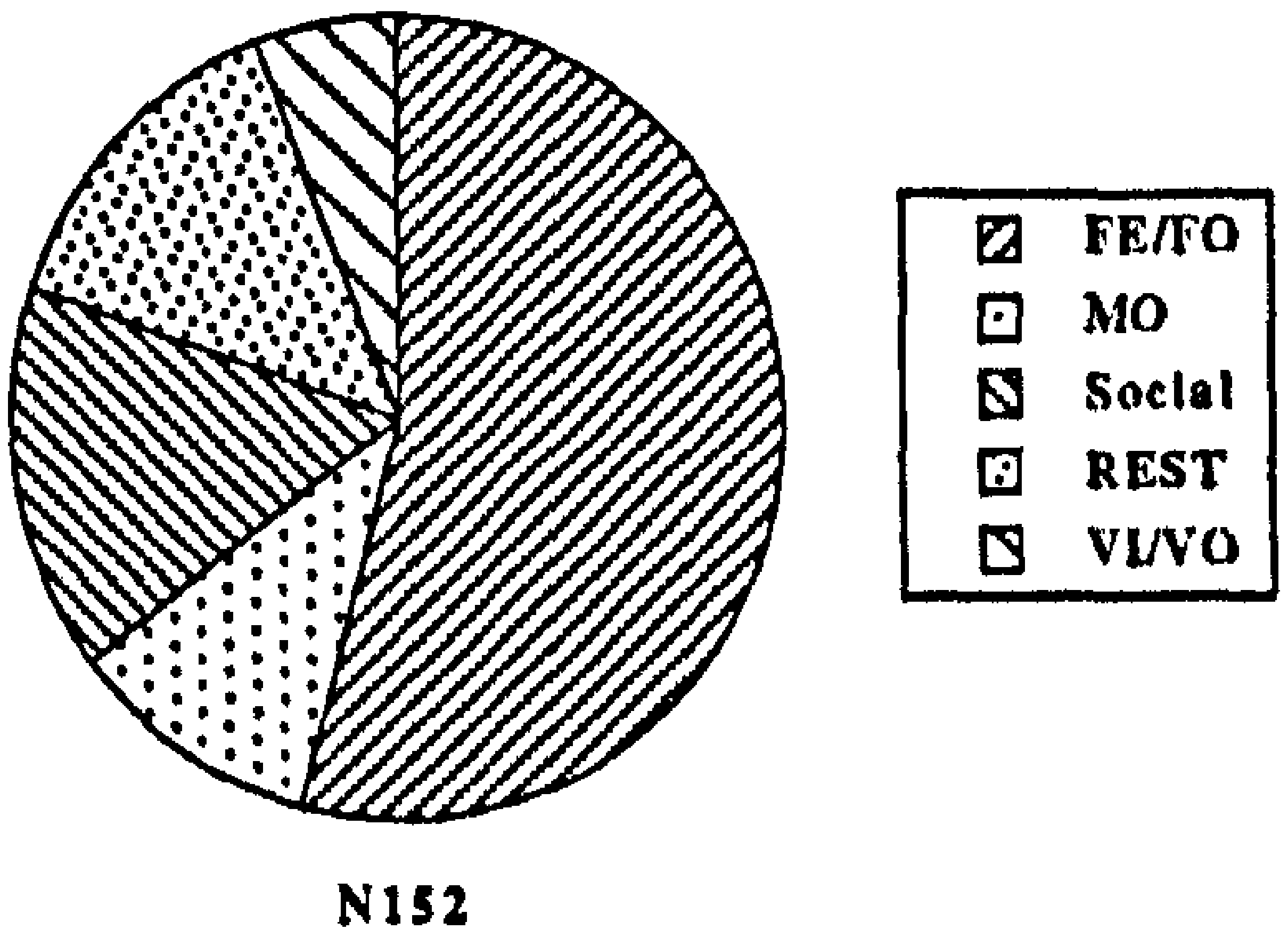


Figure 8.1.d.



Figures 8.1 a to 8.1.d Proportion of all activity scores in different activity categories for four groups: a)N32, b)N31, c)N151 and d)N152.

Codes: Fe/Fo = Feeding/Foraging; Mo = Moving; Social = Grooming, self grooming, playing; Re = Rest
Vi/Vo = Vigilant/Vocalising

Seasonal Activity

Plotting the proportion of scans in different activity categories for all two day sample periods, the seasonal activity budget of the four groups can be compared (where data was missing, mid values were used). The seasonal activity patterns of the four groups are broadly similar, all four groups showing the highest proportion of scores spent feeding/foraging followed by resting (Figures 8.2.a to 8.2.d). Both groups in N15 do show slightly more variation in the proportion of time spent feeding and foraging (see also Table 8.2). There is also a slight difference in the amount of time spent feeding and foraging during the dry season (Jan.-Mar) when groups in N15 appear to spend more time feeding/foraging while groups in N3 appear to spend more time resting/ engaged in social activities.

As a measure of seasonal variation in the proportion of time spent in different activities, the coefficient of variation for each category was calculated for all two day sample periods (Table 8.2). Groups in N3 show less variation in the proportion of time spent feeding/foraging and moving, while groups in N15 show less variation in the proportion of time spent engaged in social activities. The high coefficient of variation in vigilance/vocalising for group N32 probably reflects the unusually high levels of adult male and adult female vigilance during the male replacement and infanticide in this group (September 1994).

Table 8.2. Coefficients of variation for different activity categories (for n sample periods)

	Logged		*Unlogged*		
	N32 (n=24)	***N31*** (n=21)	***N151*** (n=22)	***N152*** (n=19)	
Feeding/Foraging	13.7	14.6	15.6	16.4	(Unlogged>Logged)
Movement	42.0	51.3	69.7	71.9	(Unlogged>Logged)
Social	43.0	38.0	32.9	34.9	(Logged>Unlogged)
Resting	58.2	78.7	67.4	69.0	
Vigilance/Vocalising	90.8	54.1	64.3	66.0	

Figure 8.2.a.

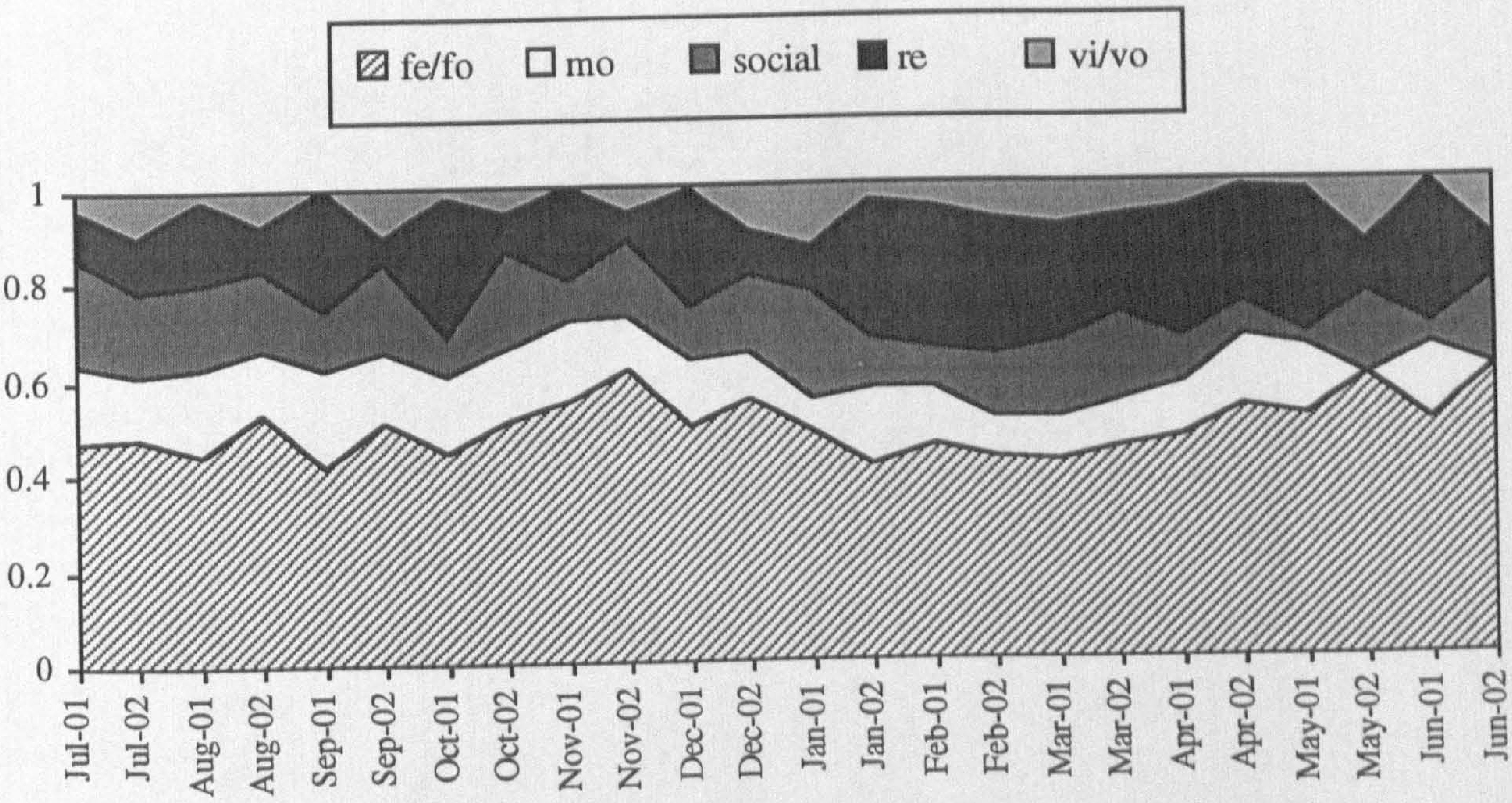
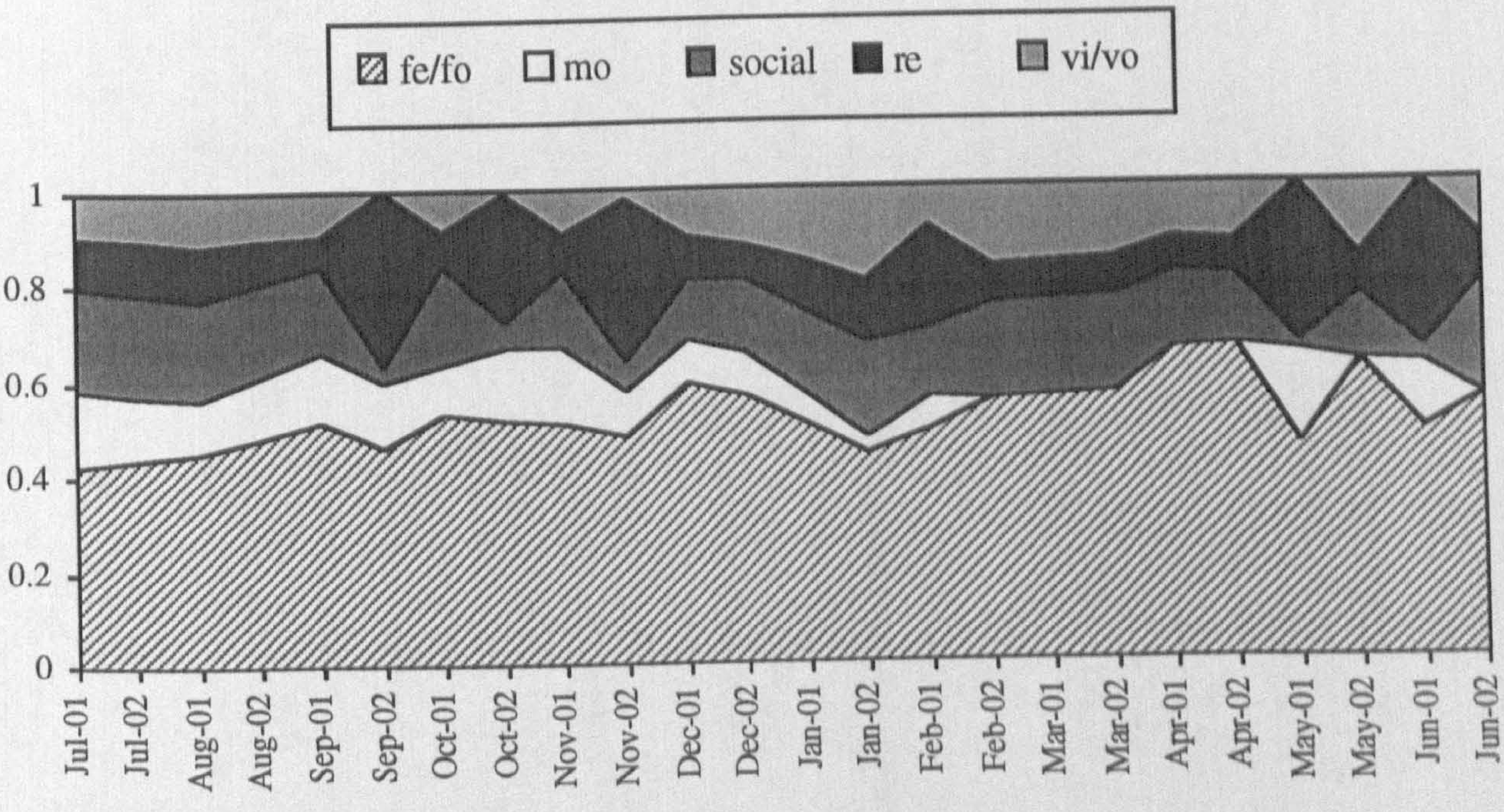


Figure.8.2.b.



Figures 8.2.a. and 8.2.b. Seasonal Activity Patterns: Group N32 (a) and Group N31 (b)

Codes: Fe/Fo = Feeding/Foraging; Mo = Moving; Social = Grooming, self grooming, playing; Re = Resting; Vi/Vo = Vigilant/Vocalising

Figure 8.2.c. (* no data for Jun 2)

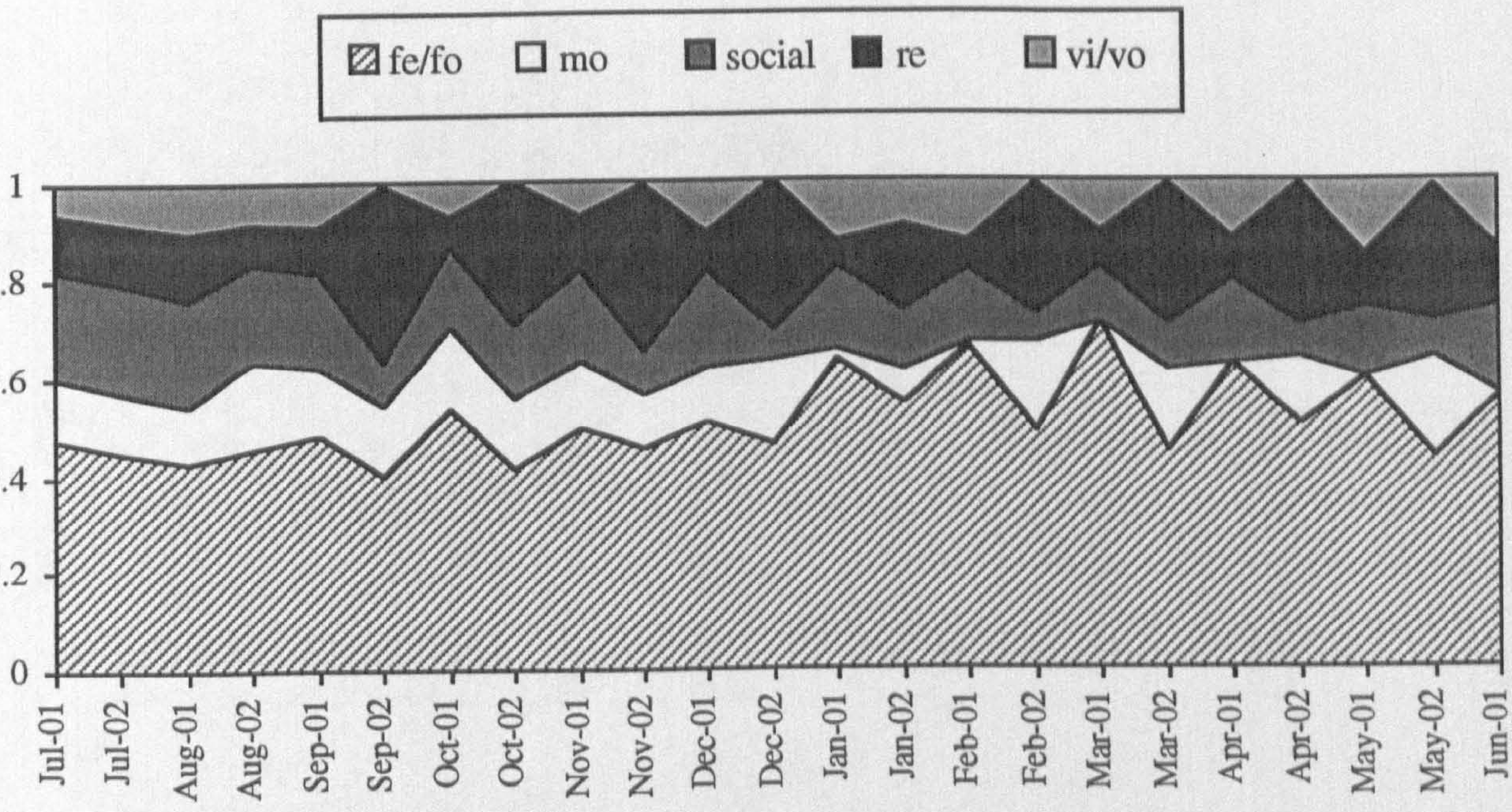
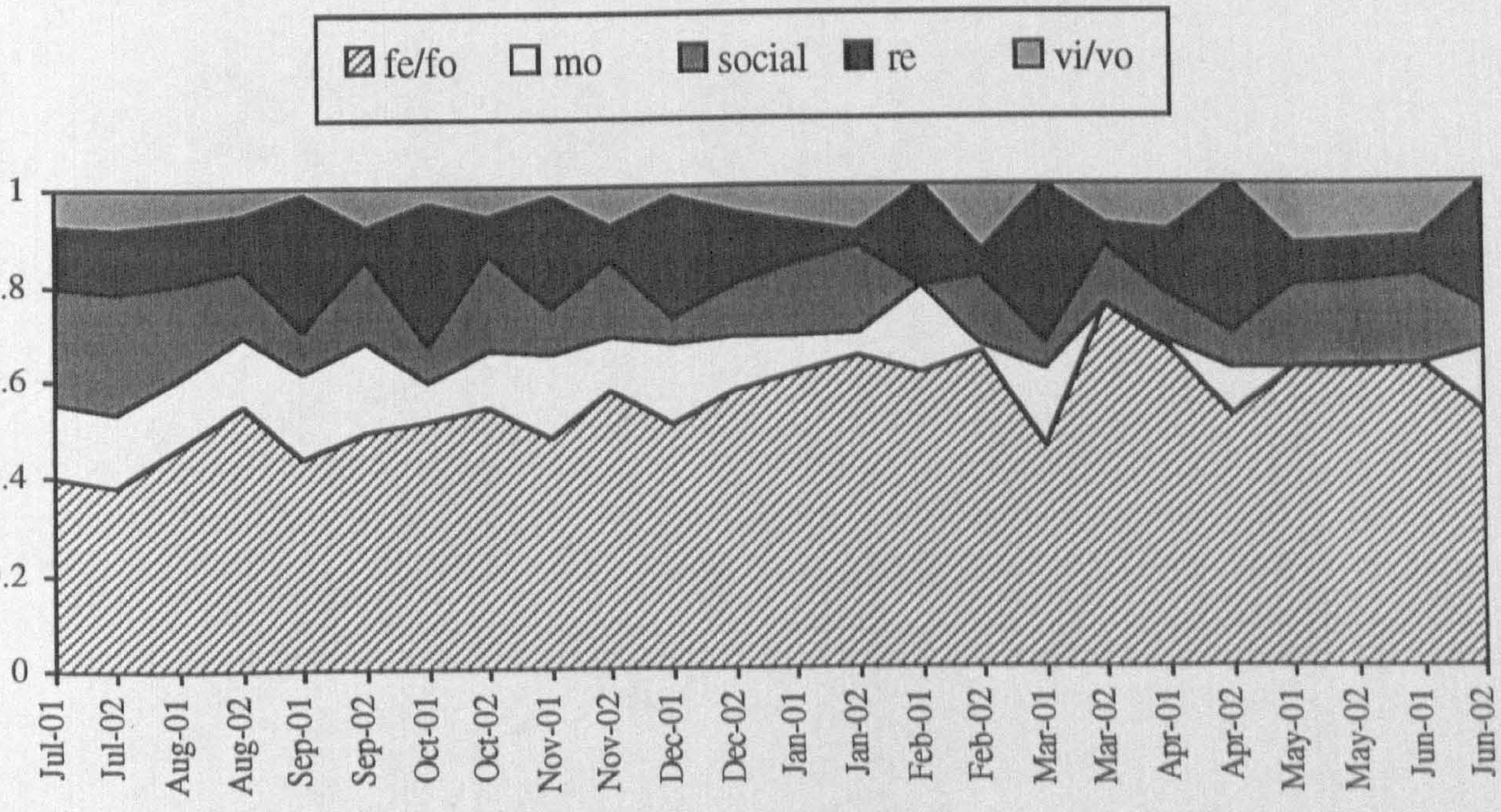


Figure 8.2.d.



Figures 8.2.c. and 8.2.d. Seasonal Activity Patterns: Group N151 (c) and Group N152 (d)

Codes: Fe/Fo = Feeding/Foraging; Mo = Moving; Social = Grooming, self grooming, playing; Re = Resting; Vi/Vo = Vigilant/Vocalising

Home Range Estimates and Ranging Patterns.

Plotting the cumulative number of new grid cells entered against the number of group location points for the four groups indicates the approximate rate of new range area accumulation over time (Figures 8.4.a to 8.4.d). Group N32 and N31 show steeper curves reaching or coming close to reaching an asymptote within the study period while the curves for groups N151 and N152 do not appear to have reached an asymptote. Groups in logged forest therefore had a more rapid rate of range size increase and this rate of increase appears to have reached an asymptote. Groups in unlogged forest however have a slower rate of increase and do not appear to reach an asymptote suggesting that the increase in range size is still occurring. This is almost certainly true for group N151 since subsequent follows by Budongo Forest Project field assistants have observed this group moving much to the west of its range as estimated in this study (A. Plumptre pers. comm.). Contact with group N152 was also lost on several occasions, and therefore it is likely that their full range is not yet known. Therefore range estimates for groups N151 and N152 are likely to be minimum estimates of their home ranges.

N3: LOGGED FOREST

Figure 8.3.a. Group N32

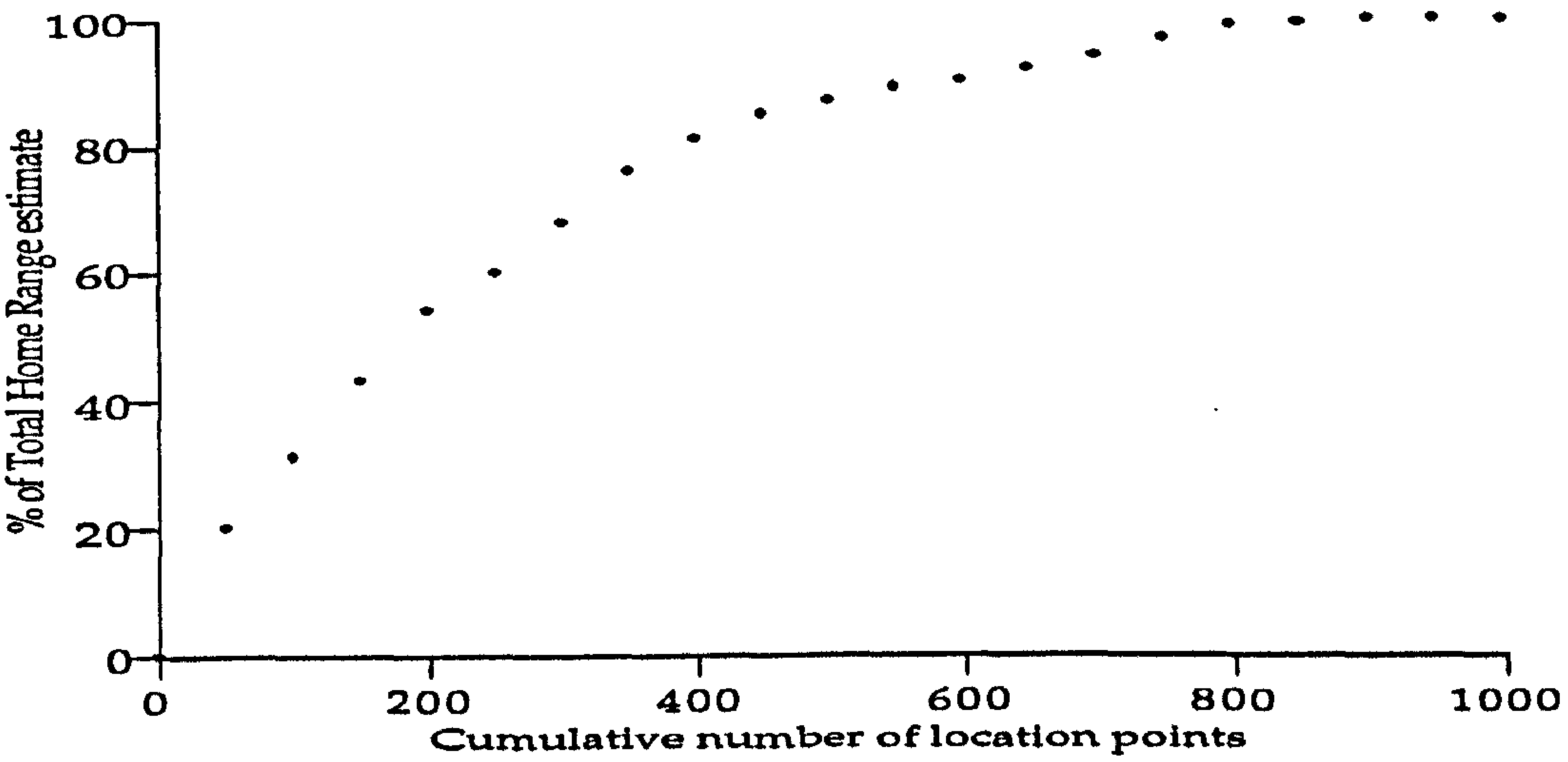
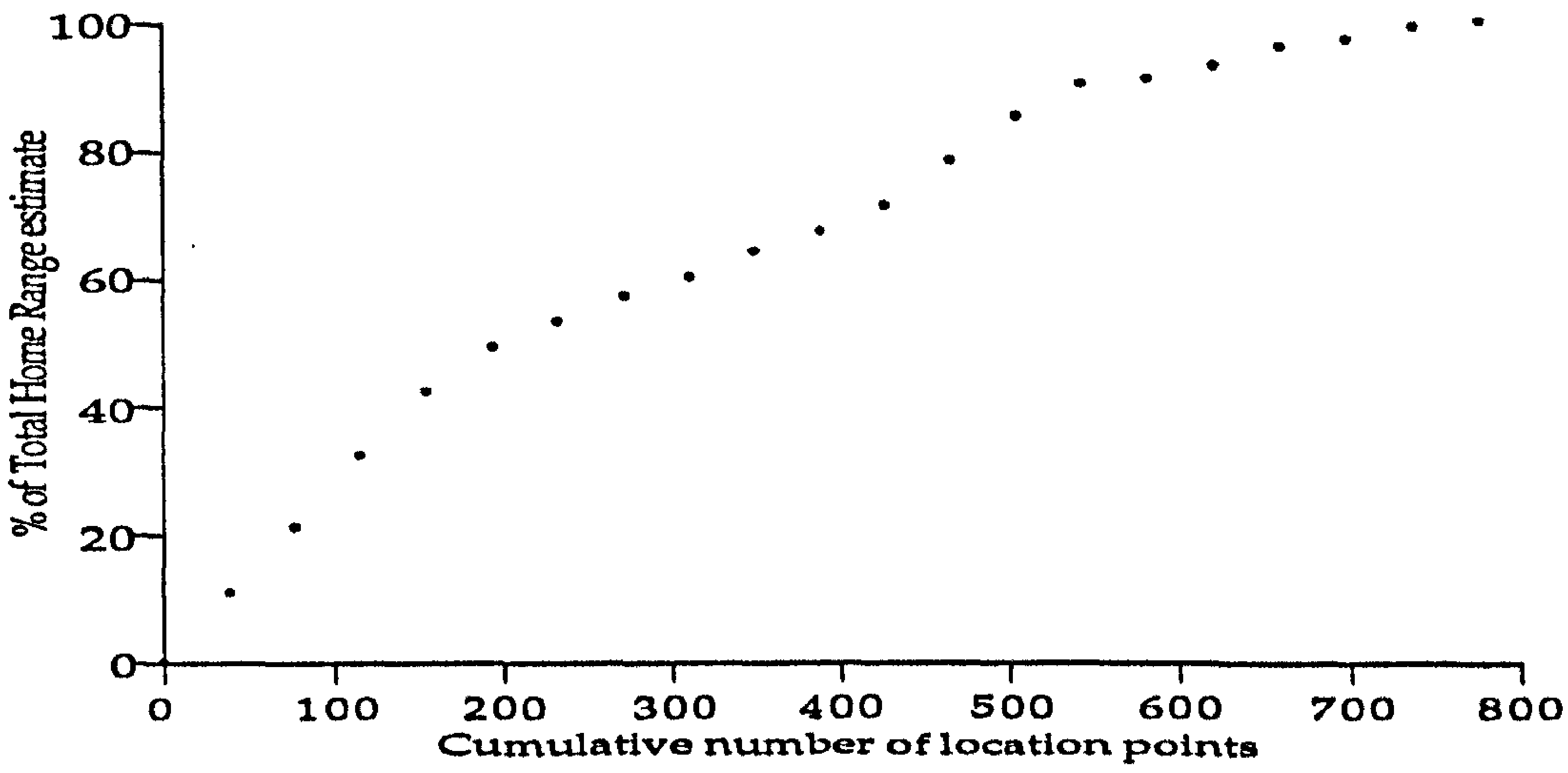


Figure 8.3.b. Group N31



Figures 8.3.a. and 8.3.b. Percentage (%) of Total Home Range area used with cumulative number of location records for logged forest groups: N32(a) and N31(b).

N15: UNLOGGED FOREST

Figure 8.4.a. Group N151

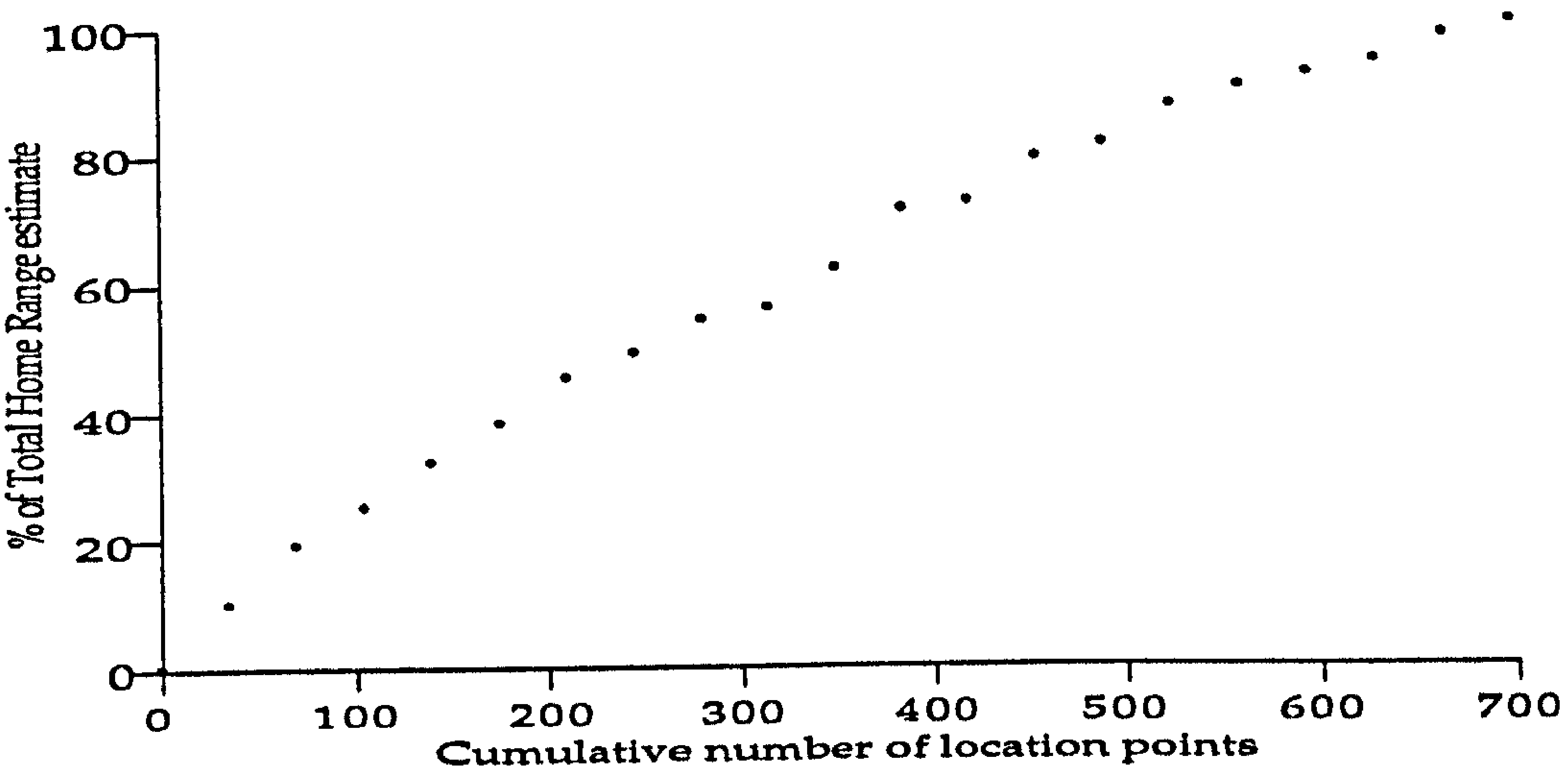
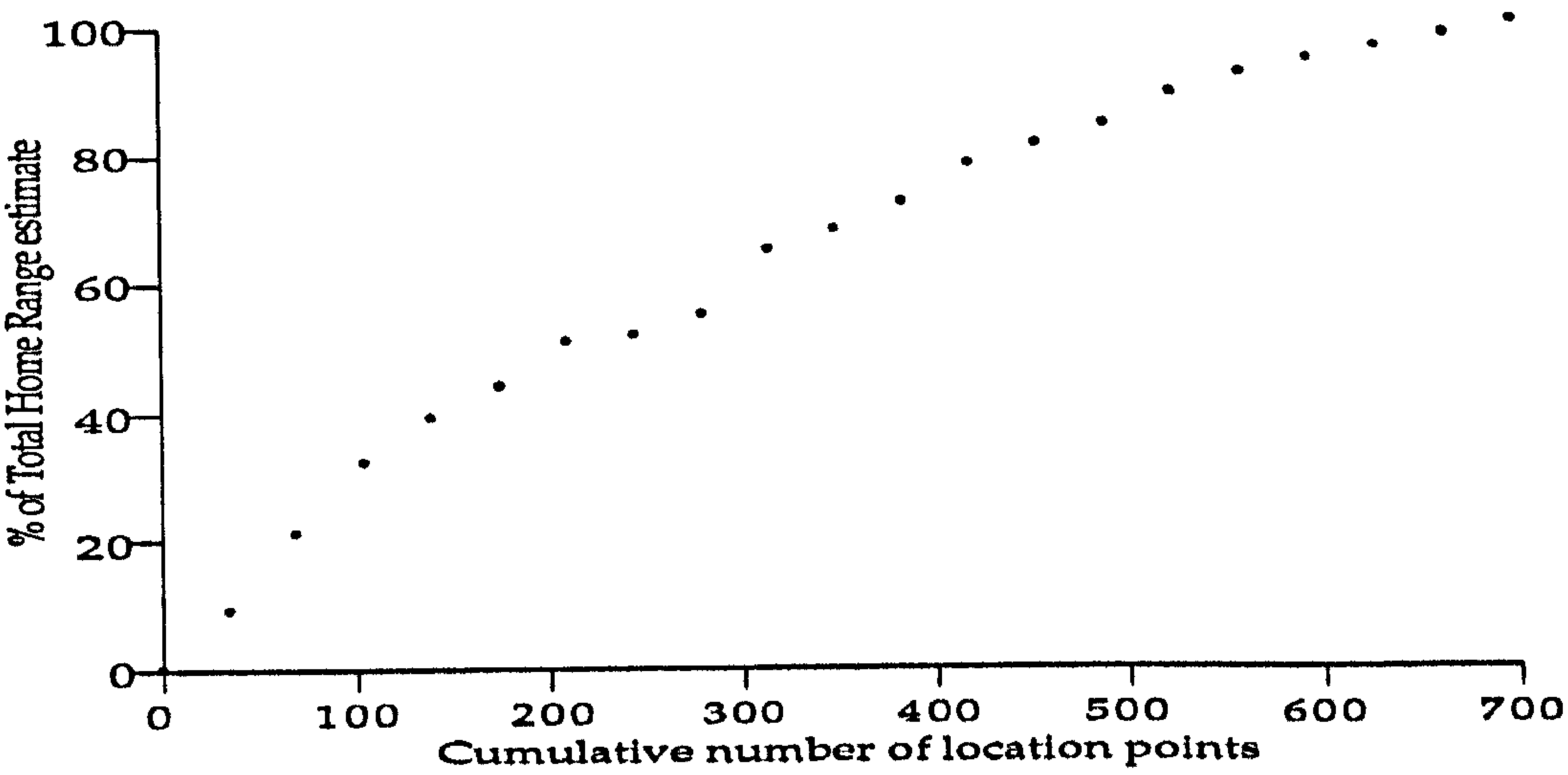


Figure 8.4.b. Group N152



Figures 8.4.a. and 8.4.b. Percentage (%) of Total Home Range area used with cumulative number of location records for unlogged forest groups: N151(a) and N152(b).

Home range was estimated using three different techniques and all estimates are shown in Table 8.3. As discussed above, the techniques give an indication of estimated territory size (restricted polygon), range use by sampled individuals within the group (grid cell) and likely range use by the whole group (grid cell with peripheral influence).

Table 8.3. Home range sizes of the four study groups estimated using three different techniques.

	Home Range Area Estimates (ha)		
Group	*Restricted Polygon (ha)*	*Grid Cell† (ha)*	*Peripheral influence† (ha)*
N32 (Logged)	8.43	8.24	12.04
N31 (Logged)	9.18	8.08	13.80
N151 (Unlogged)	19.06	11.20	23.88
N152 (Unlogged)	14.57	9.20	18.92

† 20 x 20m cells used in both cases.

Total range size estimated by all three methods is larger for both groups in unlogged forest compared to both groups in logged forest. Restricted polygon analyses and peripheral influence grid cell analyses show the largest differences in range size between logged and unlogged forest while for grid cell analyses, differences are apparent, but less distinct. This is probably because range use by grid cell analyses is likely to show the amount of actual habitat used, not the territory defended to encompass that habitat.

Restricted Polygon Estimate

Figures 8..5.a to 8.5.d show the shape and total area of the home ranges estimated using restricted polygon techniques. Ranges are plotted in relation to the trail grid system and each point represents one location record for the group.

N3: LOGGED FOREST

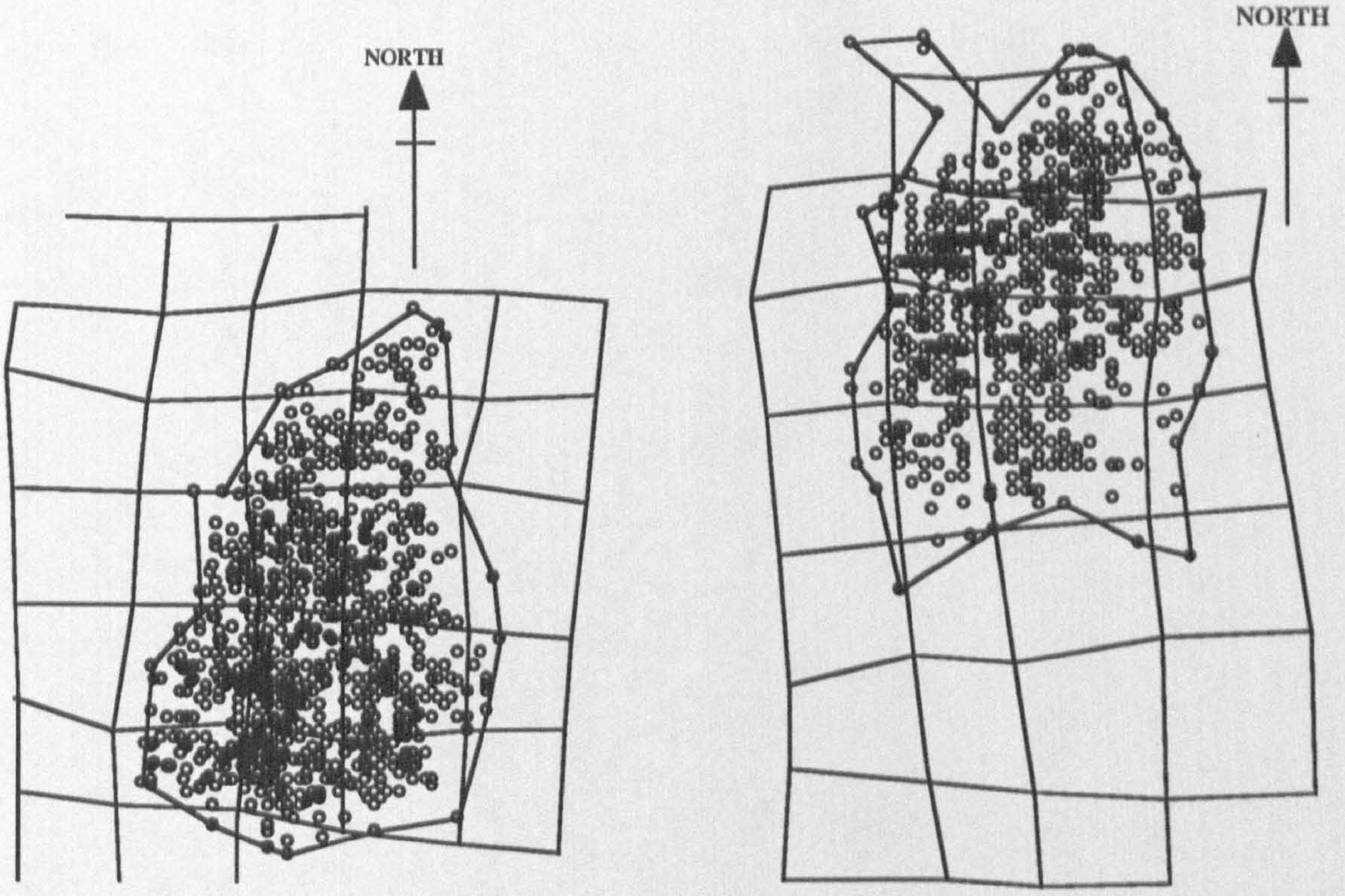


Figure 8.5.a. Group N32

Figure 8.5.b. GroupN31

Area = 8.43ha

Area = 9.18ha

Figures 8.5.a. and 8.5.b. Home range area estimated by restricted polygon technique for groups in logged forest : N32 (**a**) and N31 (**b**)

Restricted polygon estimates of range size in groups N32 and N31 (Figures 8.5.a and 8.5.b) are smaller than estimates for N151 and N152 (Figures 8.5.c and 8.5.d). The location points for groups in logged forest are also more evenly distributed throughout the range with fewer outlying location points compared to groups in unlogged forest. Both groups in unlogged forest (Figure 8.5.c and 8.5.d) show larger overall range size estimated by Restricted polygon analyses compared to groups N32 and N31. In addition, the ranges show more areas used which are outlying from the central area of the range.

N15: UNLOGGED FOREST

Figure 8.5.c. Group N151

Figure 8.5.d. GroupN152

Area = 19.06ha

Area = 14.57ha

Figures 8.5.c. and 8.5.d. Home range area estimated by restricted polygon technique for groups in logged forest : N151 (c) and N152 (d)

Grid Cell Analyses

Comparing range use by grid cell analyses gives a further indication of the shape of the range and the intensity of use of different areas. Figures 8.6.a to 8.6.d show the home range areas and intensity of use, estimated using 20 x 20 metre grid cells and plotted on the trail grid system (shading shows no. of records for the group in each grid cell). Differences in the total size of the home range estimates between groups in N3 and N15 are much less distinct, but patterns of range use appear to differ.

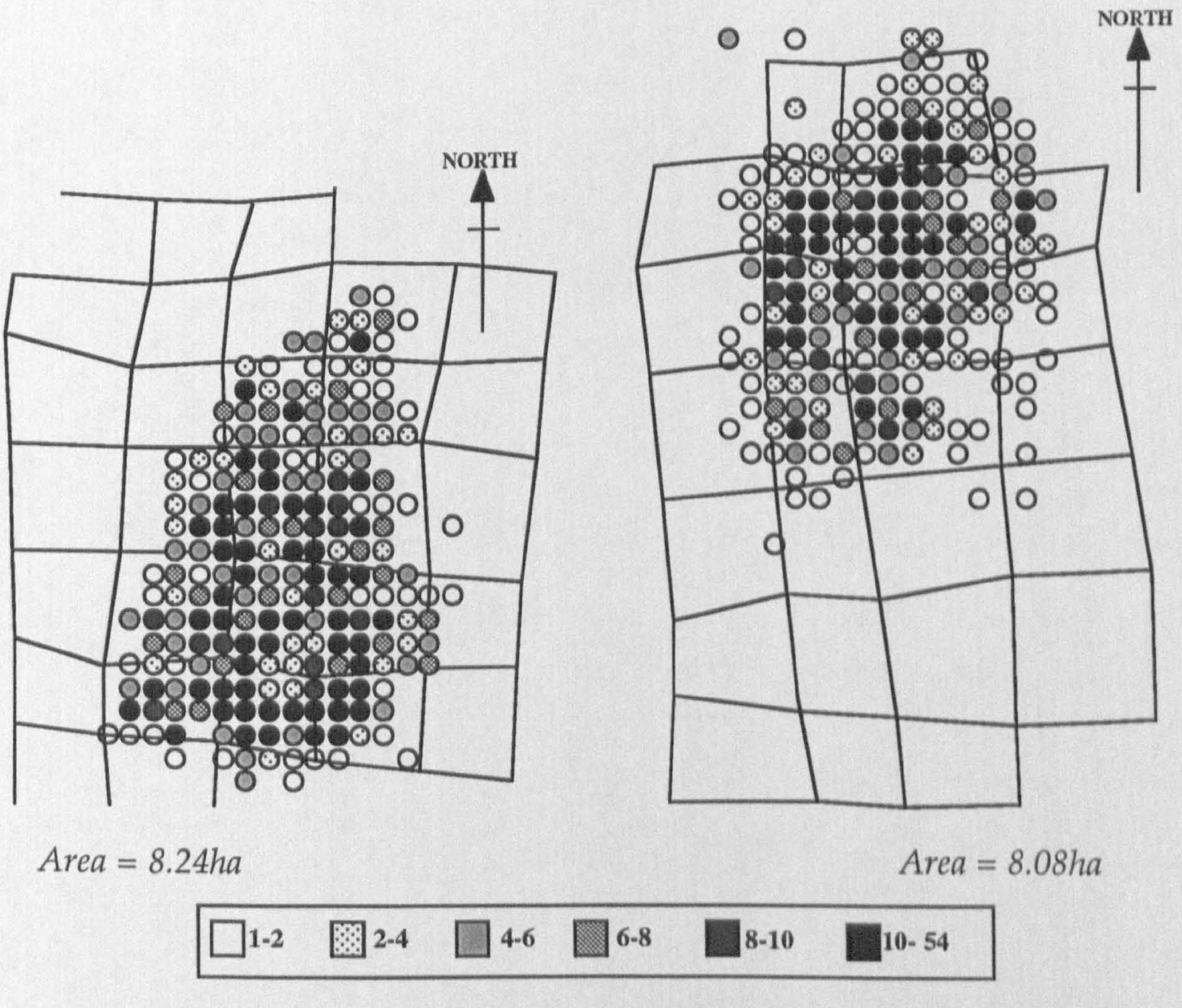

N3: LOGGED FOREST

Figure 8.6.a. Group N32

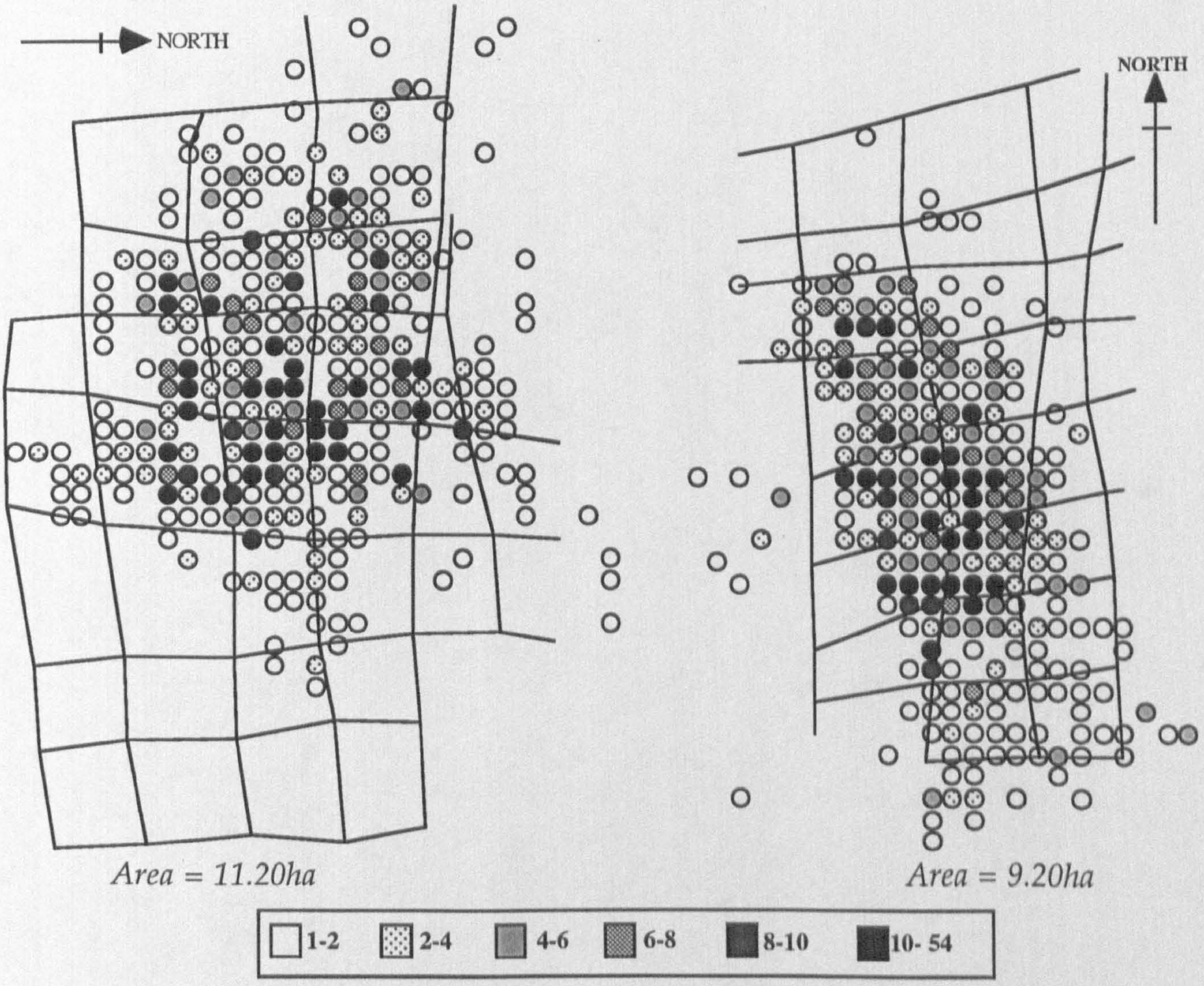
Figure 8.6.b. GroupN31

Figures 8.6.a. and 8.6.b. Home range area and intensity of use estimated by grid cell analysis for groups in logged forest : N32 (**a**) and N31 (**b**)

Both groups in logged forest show use of a much more contiguous area of grid cells which are less widely spread compared to groups in unlogged forest but show a higher intensity of use. Most of the cells occupied fall within the same central range and this central part of the range is fairly well defined by high intensity of use. Both groups in unlogged forest show use of grid cells which are much more widely spread compared to the groups in logged forest and in general show a lower intensity of use. There is a higher degree of occupation of cells outwith the central part of the range and this central part is less well defined by intensity of use.

N15: UNLOGGED FOREST

Figure 8.6.c. Group N151 **Figure 8.6.d.** GroupN152



Figures 8.6.c. and 8.6.d. Home range area and intensity of use estimated by grid cell analysis for groups in unlogged forest : N151 (c) and N152 (d)

Peripheral Cell Analyses

Estimating range use by peripheral grid cell analyses gives a smoother representation of the shape and more accurate estimate of intensity of range use for the whole group. Figures 8.7.a to 8.7.d show the home range areas and intensity of use, estimated using 20 x 20 metre grid cells with peripheral influence. Range areas are plotted on the trail grid system, shading shows no. of records for the group in each grid cell.

N3: LOGGED FOREST

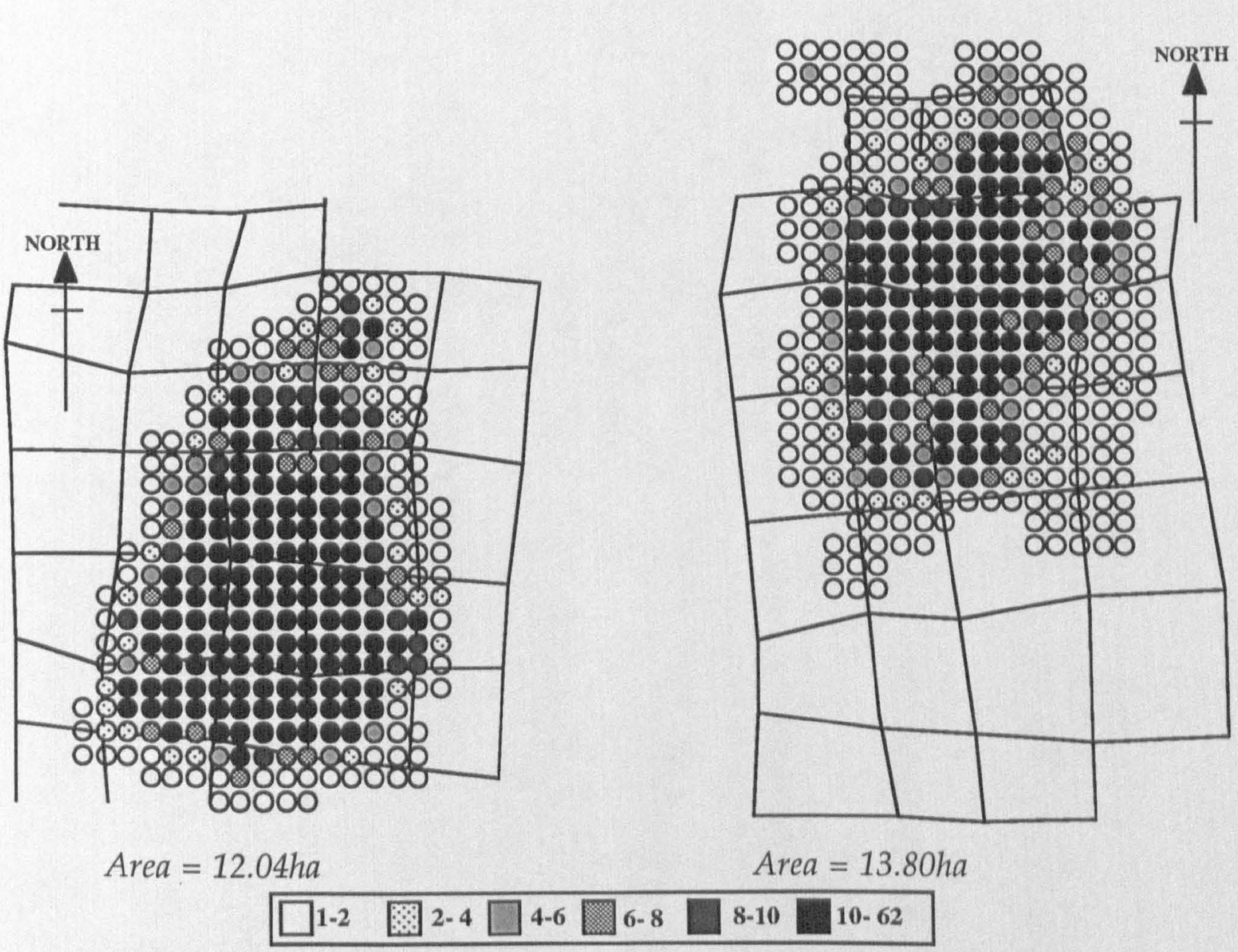


Figure 8.7.a. Group N32

Figure 8.7.b. GroupN31

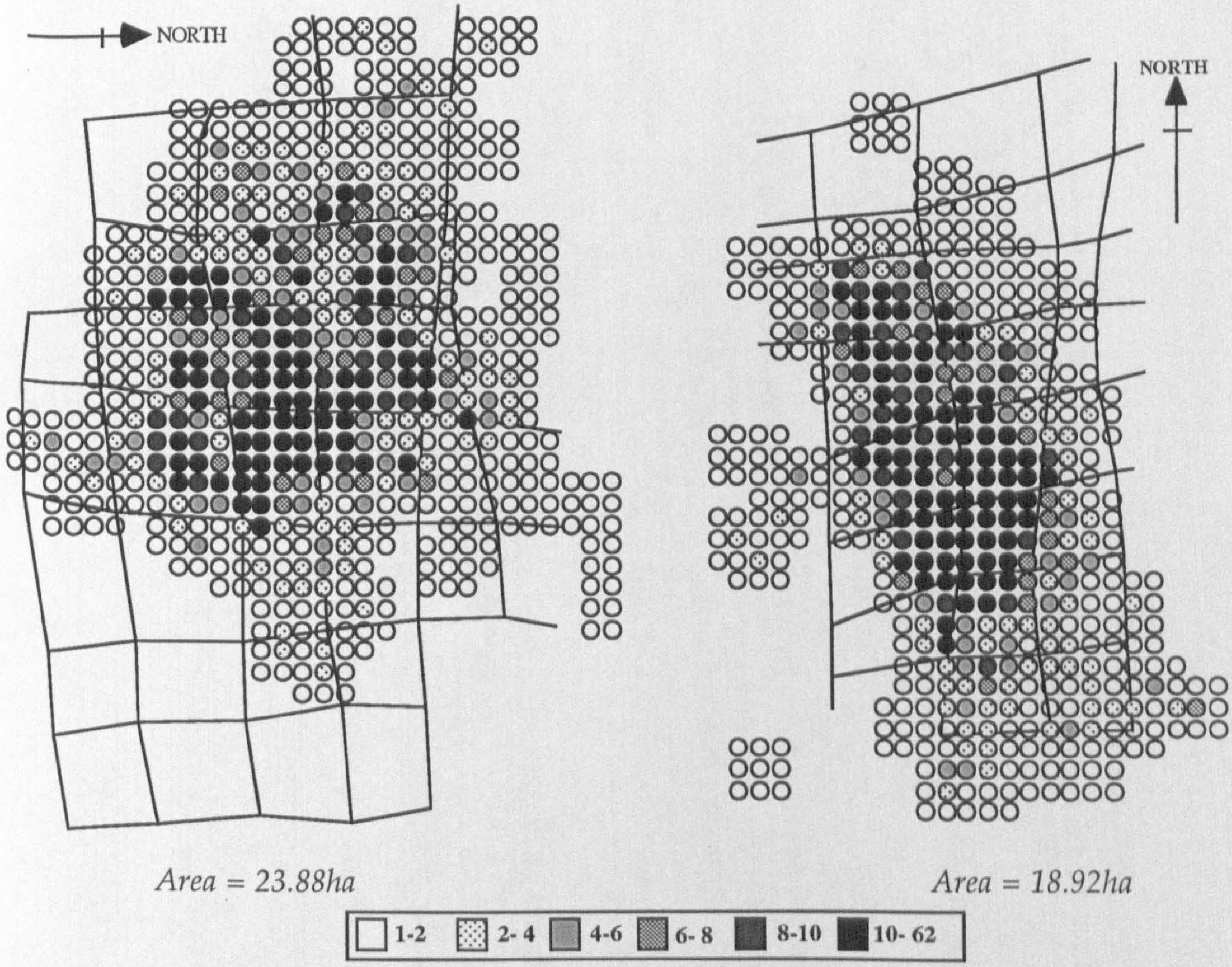
Figures 8.7.a. and 8.7.b. Home range area and intensity of use estimated by grid cell analysis with peripheral influence for groups in logged forest : N32 (a) and N152 (b)

Grid cell analyses with peripheral influence results in a much larger estimate of range size for all groups. As shown above, range estimates for groups in unlogged forest are larger compared to groups in logged forest. For groups in logged forest, a well defined core area can be seen within the range while in unlogged forest, groups do show use of a core area but this area is less well defined. In addition, overall range use is much patchier for groups in unlogged forest compared to groups in logged forest.

N15: UNLOGGED FOREST

Figure 8.7.c. Group N151

Figure 8.7.d. GroupN152



Figures 8.7.c. and 8.7.d. Home range area and intensity of use estimated by grid cell analysis with peripheral influence for groups in unlogged forest : N151 (c) and N152 (d)

Seasonal Ranging Patterns

Range area estimates for each two day sample period were calculated (in ha) using the 20 m grid cell technique and these estimates compared between N15 and N3 (Table 8.4). In addition to calculating the area of range used in hectares, this area was expressed as a percentage of the total range (as calculated by grid cell technique). Only days where more than 20 location points had been recorded were included.

Table 8.4. Home range area: area (ha) and % of total range used in each two day sample period (estimated using 20m grid cells).

Sample	*LOGGED FOREST*				*UNLOGGED FOREST*			
Period	*N32*		*N31*		*N151*		*N152*	
	area (ha)	% of total	area (ha)	% of total	area (ha)	% of total	area (ha)	% of total
Jul. 1	1.00	12.14	0.68	8.416	1.08	9.47	---	—
Jul. 2	1.00	12.14	---	---	---	—	0.68	7.39
Aug. 1	---	---	0.88	10.89	0.80	7.02	---	—
Aug. 2	1.12	13.59	---	---	0.92	8.07	0.80	8.69
Sep 1	2.00	24.27	1.0	12.38	1.04	9.12	1.32	14.35
Sep 2	1.28	15.53	1.6	19.80	1.52	13.33	1.08	11.74
Oct. 1	2.08	25.24	0.92	11.39	0.84	7.37	1.56	16.96
Oct. 2	1.20	14.56	1.68	20.79	---	---	1.08	11.74
Nov 1	2.04	24.76	1.24	15.35	0.96	8.42	1.40	15.21
Nov 2	1.24	15.05	1.72	21.29	1.56	13.68	1.04	11.30
Dec. 1	1.88	22.81	1.16	14.36	1.04	9.12	2.04	22.17
Dec. 2	1.20	14.56	1.28	15.84	1.24	10.88	---	—
Jan. 1	1.12	13.59	---	---	0.88	7.72	---	—
Jan. 2	1.56	18.93	1.16	14.36	---	---	1.08	11.74
Feb. 1	---	---	---	—	0.88	7.72	---	—
Feb. 2	1.40	16.99	1.32	16.34	1.28	11.23	1.00	10.87
Mar 1	0.88	10.68	1.32	16.34	0.92	8.07	1.24	13.48
Mar 2	1.88	22.82	1.2	14.85	1.68	14.74	1.08	11.74
Apr 1	---	---	0.98	11.88	1.00	8.77	0.88	9.57
Apr 2	1.12	13.59	1.4	17.33	0.92	8.07	1.08	11.74
May 1	1.72	20.87	1.64	20.29	0.96	8.42	1.4	15.21
May 2	1.08	13.11	1.32	16.34	---	—	---	---
Jun1	1.84	22.33	---	---	1.36	11.93	1.04	11.30
Jun 2	1.32	16.02	1.68	20.79	---	---	1.36	14.78
Mean	**1.42**	**17.19**	**1.27**	**15.39**	**1.09**	**9.44**	**1.18**	**12.60**

Comparison of two day range size using grid cell analyses (Kruskal Wallis analysis of variance) shows significant variation in the % of total home range used per two day sample period ($X^2 = 22.66$, $P<0.01$) and area used ($X^2 = 10.29$, $P<0.05$). Both groups in logged forest use a higher percentage of the total range per two day sample (Means=17.19 and 15.39 compared to 9.44 and 12.60). Comparing the area (ha) used per two days, both groups in N3 show use of a larger area than groups in N15 [1.42 ha (N32) and 1.27 ha (N31) compared to 1.09 ha (N151) and 1.18 ha (N152)].

Daily Movements.

Comparison of the mean daily path length for the four groups using a one way analysis of variance shows significant variation (F=9.607, P<0.01) between groups and both groups in logged forest have a longer mean daily path length than those in unlogged forest (Table 8.5). The percentage of all location points where groups were moving was calculated using Wildtrak. Moving fixes are a subset of all location fixes where the estimated location of the group was different from the previous location point. The percentage of moving fixes (Table 8.5) therefore gives a measure of the rate of change in location of each group. Group N32 shows the highest percentage of moving fixes followed by groups N31 and N152 (almost the same) with group N151 showing the lowest percentage.

Table 8.5. Mean daily path length and percentage of all fixes when groups were moving.

Group	Mean daily path length(m)	% Moving fixes
N32	943.90	63
N31	875.80	54
N151	691.70	49
N152	726.25	55

F=9.607, (P<0.01)

Index of Defendability (Mitani and Rodman 1979) was calculated using the diameter of the Restricted polygon area estimate and mean daily path length ($D=d/d'$). All four groups had Indices ≥ 1 which indicates capacity for territoriality. However, both indices in groups in N3 were higher than those for N15 suggesting that the costs of territoriality are lower in N3. In addition, the Index of Defendability for groups in N15 is based on minimum range estimates for these two groups (see above) therefore the actual costs of range defence (as expressed by Index of Defendability) may be higher in unlogged forest. Groups in N15 move less distance per day and have a larger area of range making the costs of territoriality higher.

Table 8.6. Index of Defendability for groups in logged and unlogged forest

	Group	*Index of Defendability* (Mitani and Rodman 1979)
Logged	*N32*	2.88
	N31	2.56
Unlogged	*N151*	1.40
	N152	1.68

Range Overlap

Comparing the overlap in the area of home range used per two day sample for consecutive sample periods shows significant differences between logged and unlogged forest. It was not possible to calculate overlap between all sample periods since some data were missing but for consecutive sample periods both groups in logged forest showed a higher degree of overlap in range use (Table 8.7).

Table 8.7. Degree of overlap in range use: area (ha) and % of previous sample range used in consecutive two day sample periods (n=no. of consecutive samples)

Group	*n*	*% of previous sample's range*	*Area of overlap (ha)*
N32	16	28.19	0.39
N31	13	27.69	0.36
N151	14	13.10	0.14
N152	13	25.14	0.29
		Kruskal-Wallis	Anova
		X_2= 18.75, P<0.001	F=14, P<0.001

Tests between pairs of groups for actual area or range overlap shows greater overlap in logged forest compared to unlogged forest (Mann Whitney U: N32/N151=8.26, P<0.01; N31/N151=6.61, P<0.01; N32/N152=3.31, P<0.01; N31/N152=2.71, P<0.01). When the % of the previous samples' range is compared, differences were significant between N151 and N32/N31 (Mann Whitney: N32/N151:U=22.5, P<0.05; N31/N151: U=20, P<0.05) but not between N152 and N32/N31.

Canopy Use

Use of different canopy heights showed some differences between the four groups probably reflecting the different canopy structure within the home ranges. Groups in logged forest spend a higher proportion of time in the low and medium canopy layers while those in unlogged areas spent more time in the high canopy layers.

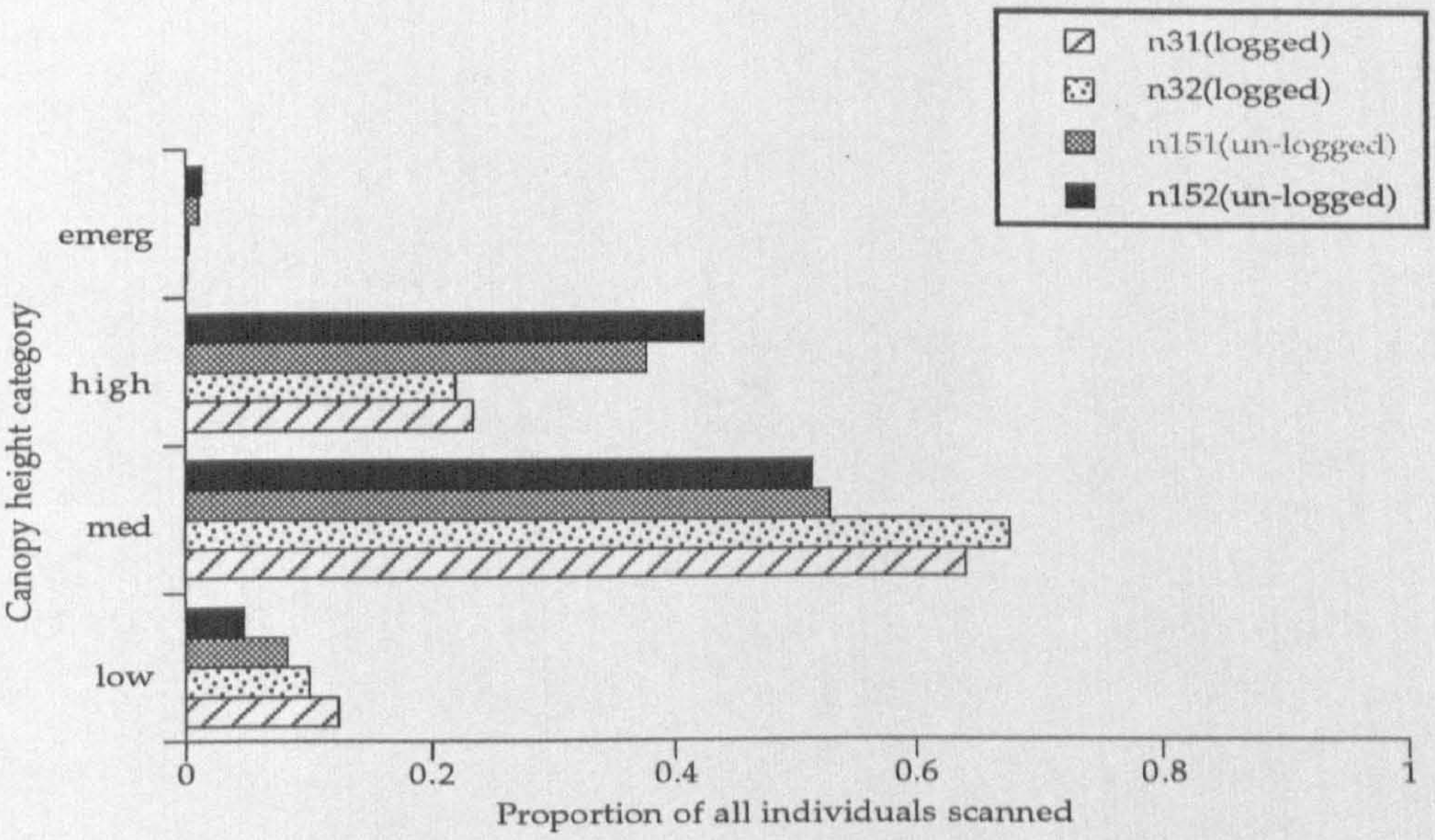


Figure 8.8. Proportion of all individuals scanned recorded in different canopy layers for all four groups

Observed use of different canopy layers can be expressed relative to estimated abundance to investigate relative use of canopy levels in N3 and N15 (Table 8.8). Although canopy use proportions were calculated for all four groups, vegetation data were only available for groups N32 and N151 so analyses were restricted to these two groups. Where heights were estimated to the nearest 5 metres (see Chapter 3 and 4), they can be grouped into canopy categories as follows:

Low.................. 0-10m
Med.................. 11-20m
High................21-30m
Emergent.........30m and above

Table 8.8 shows the proportion of stems in different height classes and the proportion of scores recorded at different canopy levels. The ratio of these two figures gives an estimate of canopy use in relation to available canopy (as estimated by proportion of stems in particular height classes). An index equal to 1 indicates a canopy layer being used in proportion to its availability. An index greater than 1 shows a canopy layer being used more than expected from its proportional abundance (i.e.. selection for that canopy layer) while an index of less than one shows a canopy layer being used less than expected from its proportional abundance.

Table 8.8. Canopy use in relation to estimated canopy availability.

	LOGGED			*UNLOGGED*		
Ht Class (m)	*Avail.*	*Use*	*Ratio*	*Avail.*	*Use*	*Ratio*
Low (0-10)	0.749	0.101	0.13	0.867	0.083	0.096
Med.(11-20)	0.181	0.677	3.68	0.096	0.530	5.52
High (21-30)	0.046	0.220	4.78	0.028	0.337	13.46
Emerg.(>30)	0.024	0.002	0.08	0.011	0.009	1.22

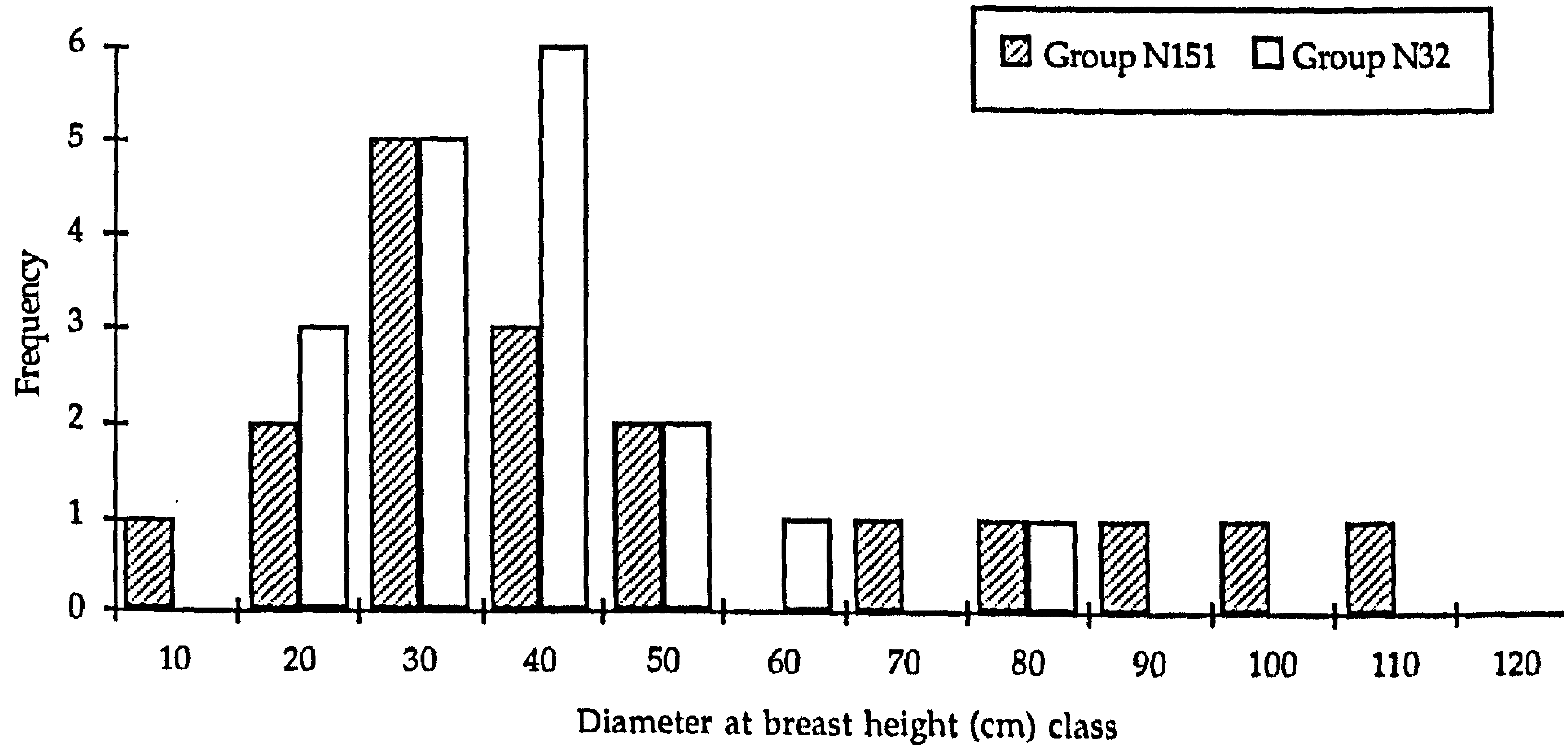


Figure 8.9. Frequency distribution by mean dbh (cm) for tree species providing main dietary items: logged forest (Group N32) and unlogged forest (Group N151).

Comparing the use of different canopy layers, it can be seen that both groups have high ratios of use : availability for the mid and high levels of the canopy, thus showing a preference for these heights. For the low levels of the canopy (0-10 metres), the ratio of use : availability is low indicating that they are used less than expected. Group N151 also shows a higher ratio of use : availability for the high/emergent levels of the canopy and more frequently uses the emergent canopy than group N32.

Comparing the main food trees in logged and unlogged forest (18 spp. providing the top 20 items for groups N32 and N151), it can be seen that individuals have higher mean dbh in unlogged forest (Figure 8.9). The individuals of the same species in logged forest occur more frequently in the mid and low canopy levels.

8.4 DISCUSSION

A comparison of activity and ranging patterns provides further evidence of difference in blue monkey ecology between logged and unlogged forest. These differences provide further evidence of the differences in habitat composition and food distribution which it is proposed are a result of logging.

Activity Patterns

Overall activity budgets are similar to those reported in other blue monkey and samango studies (Cords 1987, Lawes and Piper 1992, Rudran 1978). However, compared to other studies, blue monkeys in this study appear to spend more time engaged in feeding and 'social' activities with consequently less time spent resting (Table 8.9). The dietary quality of groups in Budongo may be higher than that reported for other sites with the result that they do not have to spend time resting to conserve energy. There is probably less inter-specific competition in Budongo compared to Kibale (as determined by the number of sympatric species: Struhsaker 1978), and there is a higher tree species diversity and stem density compared to Kakamega (Cords 1987). Both of these factors would lead to a higher food availability in Budongo compared to Kibale and Kakamega.

That groups in Budongo spend less time moving is not surprising, given the relatively small group size and the small home range area that they occupy. Lawes and Piper (1992) observed that the sum of feeding and moving activity in three *C.mitis* populations did not exceed approximately 60 % of active time. They suggested that this sum was the upper limit of these combined activities in order to maintain enough time for digestion (resting) and socialising. As shown in Table 8.9 Budongo blue monkeys do not exceed this level and spend most of the remaining time between 'social activities' and resting. The high proportion of time spent in social activities compared to other sites may imply less time required for resting and digestion of leaf material or a high degree of sociality in a small, closely related group.

Table 8.9. Activity budgets from several *C.mitis* studies.

Site/Author		*Fe/Fo*	*Re*	*Mo*	*Soc*	*Other*
Budongo †, (this study)		50.7	14.33	11.27	16.9	6.75
Kakamega, (Cords 1987)		46.5	36.1	14.1	1.4	1.6
Kibale (Butynski 1990)	Kanya.	60.3*	9.9	19.7	10.0	0.1
	Ngogo	54.7*	11.7	24.7	8.5	0.2
Cape Vidal, (Lawes and Piper 1992)		36.1	29.6	22.7	11.6	---

† Average for four groups
* (Butynski's categories of foraging, feeding and scanning summed)

No real differences in overall activity patterns exist between groups in logged and unlogged forest although some differences in seasonal trends are discernible. The proportion of time which groups in unlogged forest spent feeding and foraging was slightly higher in the long dry season and there are reductions in time spent resting as a result. Groups in unlogged forest also show higher variation in the proportion of time spent feeding/foraging and the proportion of time spent moving. This may be a result of a more patchy availability of food both spatially and temporally. Lawes and Piper (1992) stated that differences in food quality between sites may not be manifested in differences in observed feeding activity. Instead, feeding activity remains constant throughout the year but the duration of other activities will change to accommodate shifts in dietary quality. As well as food availability, temperature and daylength were important factors influencing activity budgets in samangos (*Cercopithecus mitis erythrarchus*) at their southern range limit. These parameters were assumed to be fairly constant between N15 and N3.

Johns (1985b) found that *Hylobates lar* and *Presbytis melalophos* decreased their level of activity (less time feeding and travelling, more time resting) following selective logging in Malaysia. He attributed these changes to reduced food availability and habitat fragmentation/alteration and pointed out that the ability to adjust foraging strategies accounted for the survival of populations of these two primates. Sommer and Mendoza-Granados (1995) concluded that differences in dietary quality accounted for differences in the amount of play behaviour observed in langurs. There may have been differences in activity patterns immediately after logging in N3 but it is likely that after a period of 45 years, groups have adjusted to new levels of food availability and habitat structure. The differences in activity observed between N3 and N15 are most evident in terms of i) variation in the amount of time spent in different activities and ii) responses when food abundance is at its lowest (ie. during the dry season). Greater within year variation in the time spent feeding/foraging and moving, in unlogged forest, is probably a reflection of the more patchy food distribution in space and time. The patterns of feeding/foraging in response to food availability, probably reflects different foraging strategies between logged and unlogged forest, determined again by the different pattern of food distribution.

Differences in the overall activity budget due to changes in feeding/foraging patterns are not detected and may be masked by the constraint of time spent feeding and movement not exceeding 60 % of total activity, as discussed above (Lawes and Piper 1992). Seasonal changes, as detected here, may however be equally important in terms of energy budgets and reproductive success. As well as changes in levels of activity, changes in the size and pattern of range use will reflect differences in foraging strategies between logged and unlogged forest.

Home Range Estimates

The home range estimates for the four groups are relatively small compared estimates from previous studies (see Table 2.1, Chapter 2), a reflection of the relatively small group size. A small range may also reflect the relatively high food availability in Budongo compared to other forests where blue monkeys have been studied. The accuracy of the range estimates can be assessed by calculating the expected range size from the density estimates (per km^2) for the whole compartment (Plumptre and Reynolds 1994). Estimates of 57.5 ind/km^2 and 31.2 ind/km^2 for N3 and N15 give estimates of 1.74 ha and 3.21 ha per individual monkey. For groups of 10 individuals (excludes infants) this gives range size estimates of 17.4 ha and 32.10 ha for N3 and N15 respectively. The slight discrepancy between these figures and the range estimates for the study groups (Table 8.3, Results) may be due to one of two reasons. Firstly, it may be that the estimates given by Plumptre and Reynolds (1994) are underestimates of density and the true density is higher in both compartments. This may be true for compartment N3 and has been suggested for other logged forest sites (Skorupa 1987) but is less likely for compartment N15 where actual range size (probably larger than estimated here as discussed above) is likely to approach that estimated using the above density figures. Secondly, it is also possible that the density estimates and the range estimates given here are both accurate and the difference in range size estimates is due to some unsuitable areas habitat within the compartments being unoccupied.

Overall range size estimated by restricted polygon methods is larger in N15 compared to N3. Rates of increase of range use show that range estimates are likely to be reasonably complete for groups in logged forest but are minimum estimates for groups in unlogged forest. Therefore the true differences in range size may be greater than estimated here.

Patterns of Range Use

Estimates of home range calculated by grid cell analysis are also larger in N15 compared to N3 but the difference is much less distinct. A home range estimate made using grid cell analysis is likely to give a more accurate estimate of 'habitat used' by the group. Using this assumption, it appears that groups in unlogged forest do not necessarily require a larger area of suitable habitat, but their exclusive range must be larger to encompass such habitat. The patterns of use as shown by grid cell analyses also differ between N3 and N15. Groups in N3 use their range more evenly and have a more distinct 'core area' while groups in N15 show a more patchy use of the habitat within their range area. This observation supports the proposed pattern of food distribution in logged and unlogged forest and may be important in determining the observed differences in activity patterns.

Peripheral influence grid cell analysis - estimates range use by the whole group, and smoothes this estimate - results in range estimates considerably higher in unlogged forest as compared to logged forest. In addition, groups in logged forest, as well as a smaller range, have a much more intensely used 'core area' in their ranges compared to groups in unlogged forest. This technique scores neighbouring cells around an occupied cell therefore gives a more realistic estimate of the range area used by the whole group rather than only 'estimated centre of mass' of the group.

When the amount of range used per two day sample is expressed as a percentage of the total range, both groups in logged forest use a significantly higher percentage of their total range during two day samples. The amount of range (in ha) used in each two day sample also differs between logged and unlogged forest but differences are only significant between group N32 and the other three groups. Groups in logged forest therefore appear to be inhabiting smaller ranges but using a larger % of that range during a two day sample period. It is assumed that this would lead to a more repeated use of the same areas and the more even spread of locations throughout the total home range as estimated by grid cell techniques supports this observation. As expected from this observation, the amount of overlap in range use is also higher between consecutive two day sample periods. Range overlap, calculated as the area in 20m grid cells (ha) and the % of the previous sample period's range, is greater in both groups in N3 compared to both groups in N15. Therefore over time, groups in N3 are repeatedly using the same areas of range to find food compared to groups in N15 which less frequently reuse the same areas of range. The mean daily path length (m) is longer in logged forest, again suggesting that groups there are moving greater distances during each daily sample. This distance is comparable (For four groups Mean = 809.41 m) to Kakamega, where Cords (1987) reported a mean daily path length of 1136 ± 228 m for a larger group of 32.6 blue monkeys in a larger home range (range size = 23 ± 9 ha).

The Index of Defendability (Mitani and Rodman 1979) shows that all four groups have ranges which are defendable according to this model. However, groups in unlogged forest show indices which are much closer to 1 indicating less defendable ranges and potentially higher costs of territoriality. If the range estimates are minimal (see above) and the true range is actually larger in unlogged forest, then the costs of territoriality are likely to be higher in N15.

Differences in home range area were documented by Butynski (1990) in neighbouring populations of blue monkeys in Kibale Forest. He concluded that this was not due to differences in food availability but suggested that one population was very much below carrying capacity and therefore experienced a surplus of available habitat. He also concluded that in the low density population (Group 33) there was a tendency towards non-territoriality due to high energetic costs. Johns (1986) observed 'remarkably little change' in the home ranges of *H.lar* and *P.melaphos* following logging although there was some degree of shift in the pattern of range use. The ranging patterns shown by groups in this study indicate that logged forest is a more productive habitat both spatially and temporally resulting in a smaller total area of range which is used more intensely. Harrison (1983) stresses that slowly renewing resources which have a sparse distribution are important determining the lower limit on home range size and site. Where a range is being used more intensely over time this may indicate that the rate of resource renewal is faster in N3 compared to N15.

Foraging Strategies

Gautier Hion (1988) describes guenon ranging strategy as a selective one: if food availability is high then range use will be concentrated in an area of the range with high food tree density. If food is less abundant then ranging will focus on individual trees with high food availability which are dispersed throughout the range. During the dry season when food resources are scarce, feeding tactics rely on the densest fruiting species at the expense of dietary diversity. When the diversity of fruiting species is greater, blue monkeys (and other guenons) are more likely to be selective and concentrate on areas which contain several fruiting species. With fruit availability much higher but variable throughout the year in logged forest compared to unlogged forest (Chapters 6 and 7), it is likely that groups in logged forest will concentrate their ranging more often on range areas of high density of fruiting individuals. Groups in unlogged forest, where fruit availability is more limited, would be expected to concentrate their ranging patterns on densely fruiting individuals distributed throughout the range.

Reviewing the literature on feeding behaviour in C.*mitis* during periods of food shortage, Lawes et al (1990) suggested the following foraging pattern. When food availability is low, monkeys increase their feeding time, use poorer quality food (eat more foliage) from more abundant tree species and conserve energy by moving more slowly about the home range. As seen in the previous chapter, groups in unlogged forest probably make use of poorer quality foods and despite the lack of significant differences in overall activity budgets, they do increase the amount of time spent feeding/foraging in response to such food shortages. Range use compared between logged and unlogged forest indicates lower food availability in unlogged forest. In logged forest however, due to the different spatial and temporal food availability activity budgets and ranging patterns do not fit this model. Instead, groups in logged forest decrease the amount of time spent feeding foraging in response to low food availability perhaps conserving energy and maintaining dietary quality by feeding on unripe fruit.

If food availability is important in determining the home range area and the foraging strategies of groups, then it appears that the higher and more constantly available range of food resources in logged forest may be one of the key factors leading to an increase in density.

Canopy Use

It appears that differences in canopy structure between logged and unlogged forest do not result in major differences in movement pathways of groups in N3 and N15. Kaplin (pers. comm.) observed that *C.mitis* in Nyungwe forest, Rwanda did not travel on the ground in natural open areas of their range, but skirted round the edge while still moving in th canopy. This may suggest a preference for moving in the canopy due to the presence of ground predators. In Budongo, blue monkeys were only observed moving on the ground on two occasions (once during the male-infanticide, Group N32 and once while eating guinea fowl eggs, Group N151). It is likely that canopy cover in logged forest in Budongo approaches that of unlogged forest therefore movement pathways are probably very similar for groups in logged and unlogged forest.

Comparing vertical use of canopy between N3 and N15, there are differences in the proportion of time spent in different canopy levels. Groups in N3 spent a higher proportion of time in the mid/low canopy levels while groups in N15 spent more time in the high and emergent canopy. Expressing use of canopy relative to canopy availability (estimates are for groups N151 and N32 only), group N151 selects for the emergent and higher canopy while group N32 selects only slightly for the mid and high canopy levels. This difference in canopy use is probably due to differences in vertical forest structure between the two compartments and differences in the height of food trees. As shown in Figure 8.9, individuals of food trees used by both groups are likely to be larger in unlogged forest, therefore it is not surprising that groups in unlogged forest spend a higher proportion of time in the high and emergent canopy. In addition, the more uniform nature of the higher and emergent canopy levels in unlogged forest may provide more suitable movement pathways and cover against predators. Food trees in logged forest are more likely to be smaller than those in unlogged forest and in addition, the emergent canopy is likely to be much more patchy while the mid and high levels will be more structurally uniform. Therefore groups in logged forest would be expected to spend a higher proportion of time in the mid and high levels of the canopy where food is and movement pathways are available and cover from predators can be sought.

Conclusions

i) There are no significant differences in overall activity patterns between groups in logged and unlogged forest. There are however differences in the seasonal activity patterns with groups in unlogged forest showing a higher amount of variation in time spent feeding/foraging and resting. Differences in food availability and distribution in the habitat may be important in determining the differences in activity patterns.

ii) Groups in unlogged forest occupy larger home range areas (as shown by three methods for calculating home range area), use their range less intensively and travel less distance per day compared to groups in logged forest.

iii) It is likely that these differences in range area and patterns of range use reflect a more suitable habitat for groups in logged forest where food availability is higher and food resources distributed more evenly.

iv) Canopy use by groups in logged and unlogged forest shows some differences, the proportion of time spent in different canopy layers reflecting different canopy structure in logged and unlogged forest.

CHAPTER 9

GENERAL DISCUSSION

In the preceding chapters I have described differences in forest composition, forest structure and phenological patterns of plant part production, between logged and unlogged compartments. Evidence has been presented to suggest that these vegetation differences account for differences in diet and ranging patterns of groups of blue monkeys (*Cercopithecus mitis stuhlmanni*) and may ultimately lead to differences in population density in the two areas. The group counts obtained from this study show relatively small groups in Budongo compared to other sites, and this is indicative of a high availability of food resources distributed evenly throughout the habitat. Despite the difference in density and range size between logged and unlogged forest, group size does not appear to differ.

In addition, it is proposed that the observed differences in vegetation and blue monkey ecology are a direct or indirect result of logging. The processes which are likely to have resulted in these differences are discussed below and a hypothesis for blue monkey population density increase is proposed. The results are also discussed in the context of tropical forest management designed to satisfy timber production and biological conservation goals.

Habitat Differences Between Logged and Unlogged Forest

The most striking differences in vegetation composition and structure between logged and unlogged forest are i) a significantly higher tree species diversity per unit area in logged forest compared to unlogged forest and ii) a high proportion of colonising tree species in logged forest compared to unlogged forest. In terms of biomass (Basal area per unit area), logged forest is strikingly similar to unlogged forest (only 6.96% less Basal area per unit area) and indeed has a higher stem number per unit area although this difference is not significant. In addition, there are higher proportions of stems in the mid range of dbh classes in logged forest while unlogged forest shows a higher proportion of stems in the small and large dbh classes. Tree species in logged forest are more characteristic of colonising forest (Synott 1985) and are it has been previously suggested that these type of species are fast growing and have a high rate of production of reproductive parts [fruits and flowers] (Johns 1991b, Rodman 1978). In unlogged forest by contrast, there is a lower tree species diversity and the dominant species *Cynometra alexandri* is very abundant, together with several other tree species - *Lasciodiscus mildbraedii, Entandrophragma spp., Celtis mildbraedii, Celtis zenkerii* - associated with Cynometra-Mixed forest. Many of these species are characteristic of climax forest (Eggeling 1947a) and it has been suggested that these species have high levels of production of vegetative plant parts [leaves and buds] (Johns 1991b, Rodman 1978). A high proportion of the fruits and seeds which are produced in unlogged forest are wind dispersed or scatter dispersed and are not commonly fed on by blue monkeys and other frugivores.

Tree species associated with colonising forest are common in logged forest and contribute greatly to the Importance Value estimate for the top 20 species. Some of the same species do occur in unlogged forest, but do not contribute greatly to the Importance Value estimates (Chapter 4) and are probably limited in distribution to natural gaps (Synott 1985). Logging with an appropriate felling intensity, followed by a sufficient time period for regeneration of forest cover to occur, may therefore create more suitable conditions for tree species associated with colonising forest. The resultant forest cover may also have a more varied canopy structure and show more within-habitat structural variation. Forest post-logging is therefore, a more heterogeneous forest type with higher tree species diversity and a more even distribution of biomass (estimated in terms of Importance Values) among tree species compared to unlogged forest (Chapter 4).

As well as differences in the tree species composition and abundance, there are differences in the production and availability of plant parts which feature regularly in the diet of blue monkeys (Chapter 5). The annual production of leaves fruits and flowers in both N3 (logged forest) and N15 (unlogged forest) is noticeably seasonal and appears to be closely related to rainfall. Within this annual pattern there are seasonal differences between the two compartments for the species being regularly eaten by blue monkeys. Unripe fruit production and youg leaf production during the wet season is higher in logged forest compared to unlogged forest, and several Ficus species which are absent from logged forest appear to provide 'keystone food resources' in logged forest during the dry season. Estimates of fruit availability are higher throughout the year (they are however more variable) in logged forest compared to unlogged forest while estimates of leaf production are higher (but more variable) in unlogged forest compared to logged forest.

The higher tree species diversity, greater range of edible fruits and increased phenological productivity, all effectively increase the overall annual fruit availability in logged forest. A dry season (December-March) reduction in food availability is observed in both logged and unlogged forest (for important food items). However this periodic shortage probably represents less of an 'ecological bottleneck' (Terborgh 1986) in logged forest by virtue of the peak in production of unripe fruit in several *Ficus* species and other tree species which occur in logged forest. The vegetation in logged forest in Budongo is therefore likely to be a much more suitable habitat for a generalist/frugivore primate like *C.mitis*. Habitat suitability can be reflected in terms of how closely a primate's diet meets its nutritional needs and whether dietary shifts occur throughout an annual cycle or during periods of low food availability.

In the context of discussing habitat suitability, several dietary differences between logged and unlogged forest were observed. Firstly, a higher level of fruit is present in the diet of logged forest groups and in addition, groups in logged forest show less variability in the seasonal pattern of fruit intake. This is probably due to the higher and more constant availability of fruit in the ranges of these two groups. Groups in unlogged forest by contrast have a lower overall intake of fruit and at certain times of the year they must supplement their diet more with young leaves, flowers and seeds. There is no real difference in dietary diversity but groups in logged forest rely on fewer items (usually ripe and unripe fruit) for the bulk of their dietary intake while groups in unlogged forest depend on a wider range of dietary items. Based on the assumption that fruit is a high quality part of the diet, it may be that groups in logged forest are able to maintain a higher quality diet throughout the year. The importance of fruit as a limiting resource for guenons has been reported (Gautier Hion 1988, Lawes 1991) so fruit intake is likely to be very important in determining dietary quality. It is proposed that dietary quality is higher in logged forest due to the suitability of habitat and that this is reflected in the dietary composition of the groups in logged forest. The long term consequence of this increased dietary quality may be an enhanced female fecundity, which may ultimately result in higher rate of population growth in logged forest compared to unlogged forest.

The tree species producing the fruit items important in the diet of groups may be more abundant and exhibit a clumped pattern of distribution in logged forest. These same tree species are less abundant and follow a more scattered distribution in unlogged forest. As a result, groups in unlogged forest show a stronger degree of within habitat 'selection' at all times of the year when feeding on the major items in their diet. This is especially noticeable during the dry season, which appears to be a period of food shortage for groups in unlogged forest. This pattern of feeding reflects a lower food availability in unlogged forest and suggests that food resources are more sparsely distributed in unlogged forest. In addition, ranging patterns (see below) will be determined largely by the distribution and abundance of important food trees.

As discussed earlier, several studies have presented evidence to support the observation that food availability (and ultimately range requirements) are important determinants of primate population density (Cant 1980, Lawes et al 1992, Oates et al 1990, Pinto et al 1993). Oates et al (1990) discussing this hypothesis alos observed that in Tiwai (Sierra Leone) folivore biomass is high in a forest showing very distinct seasonal patterns of leaf shedding during the relatively long dry period. They argued that primate densities are more likely to be determined by the availability of subsistence foods during ecological crunches than the availability of high quality food items. Butynski (1990) also discussed the influence of food availability on population carrying capacity and although blue monkey density in his study was likely to have been influenced by a disease outbreak, he recognised the role of food availability and range requirements.

In this study, differences in diet which may be directly related to vegetation changes following logging are likely to have important consequences for dietary quality and ultimately influence female fecundity and population density.

Differences in ranging patterns

To assess the evidence for food availability as a determinant of carrying capacity, activity budgets, range size and range use were also investigated. Chapman (1988) discussed the difficulties in discerning determinants of foraging patterns and concluded that in most cases the responses of primate species to changes in seasonal food availability were complex. This study provides evidence relating to the nature and quality of the diet, together with the observed ranging patterns, to suggest that the density increase in logged forest is in response to a more productive habitat in terms of blue monkey foods.

It is widely believed that ranging patterns in primates reflect the overall availability and the patterns of availability of food throughout the year (Gautier-Hion 1988, Garber 1987, Leighton and Leighton 1983). Groups in logged forest show a more intensive pattern of use of a small range while in unlogged forest range use is more patchy in space and time and the total home range is larger. This suggests a higher availability of food resources dispersed evenly throughout the range in logged forest but fewer, more over dispersed patches of food in unlogged forest. The estimate of home range size in unlogged forest may even be an underestimate and the actual difference in range size and patterns of use may be greater. It seems therefore, that there is a real effect of higher food availability on range requirements and habitat carrying capacity in logged forest. As well as range use being more even, the groups in logged forest also utilised a higher proportion of their total range per sample period and moved further during one day's ranging. This reflects the fact that these groups are able to re-use the same areas of the range more frequently indicating i) higher overall availability of food items and ii) a potentially higher rate of renewal of food resources within the range (sensu Harrison 1983).

Activity budgets do not differ significantly overall but some seasonal differences are detectable. Groups in unlogged forest show more variability throughout the year in the proportion of time engaged in different activities. Lawes et al. (1992) suggest that *C.mitis* will be expected to either increase searching time or reduce selectivity/minimise energetic expenditure in response to food shortages. Groups in logged and unlogged forest appear to show different responses determined by the distribution and abundance of food resources within their range. The response of groups in unlogged forest is indicative of a lower overall food quality and the inability to incorporate a shift in diet and still maintain a high enough dietary quality. Groups in logged forest appear to be more flexible in their foraging strategy ie. with changing food availability they can maintain a sufficiently high nutritional intake and not have to change the amount of time spent feeding/foraging or adopt energy conserving measures.

How does Density Increase ?

Assuming that other factors such as predation, competition and disease are constant in both logged and unlogged forest, and considering the evidence presented in the preceding chapters, the following hypothesis is suggested as an explanation for the difference in observed population density between N3 and N15.

Firstly, changes in the tree species composition and vegetation structure result following timber extraction and the accompanying habitat disturbance. These vegetation changes lead to higher tree species diversity and an increase in the abundance of colonising species in logged forest as compared to unlogged forest. In terms of blue monkey food resources, this translates into a overall higher food availability for blue monkeys with notable increase in quality foods (fruit). Combining this with the observed changes in timing of phenological production results in an observed increase in food availability during the year, notably during the period of the year that is normally the period of food shortage (dry season). An increase in blue monkey group size is therefore predicted due to an increase in female fecundity and population growth rate. One question which arises at this point is why does population density show clear differences between logged and unlogged forest, but groups size remains fairly similar ?.

This may be accounted for by the fact that an increase in group size may have an upper limit beyond which group fission is expected to occur due to a range of socio-ecological factors. Such patterns of group increase followed by fission and subsequent reduction in range size has been observed for blue monkeys and other forest primates (Cords and Rowell 1986, Lwanga 1987, Malik 1986). Describing the process of fission in a blue monkey group in Kakamega forest, Cords and Rowell (1986) suggested overcrowding (i.e. shortage of resources) as the main factor driving group fission. In those circumstances, a large group of 46 individuals (range size 31.75 ha) split into two groups of 33 and 13 individuals occupying 23ha and 15ha of home range respectively. Menard and Vallet (1993) documenting group fission in *Macaca sylvanus* again suggest 'overcrowding' as the ultimate cause and discuss this in terms of social cohesion and intra-group competition. Previous accounts of multi-male influxes in *C.mitis* have occurred in groups of large sizes [n=30, Henzi and Lawes (1987); n=69, Cords et al (1986)] and may be an indicator of a breakdown of social cohesion resulting from the increasing size of the group. It is likely that there is an optimum group size in *C.mitis* in Budongo (as well as throughout the range of other habitats occupied) which is determined by the distribution and abundance of food resources, ability to maintain social cohesion and predation pressure.

The process of fission may therefore have resulted in the formation of two smaller groups which were able to more effectively defend an adequate range and 'function' socially. In addition, since the habitat was more productive in terms of food items for blue monkeys, a smaller total range would suffice to satisfy the ranging and feeding requirements of these two new groups. This range would not only be smaller than the range used by the group pre-fission but will be smaller than the range required by a group of similar size in unlogged forest. In this way, it would be possible for more groups to occupy the same area of habitat and so experience an increase in population density in that forest type subsequent to logging. Factors such as inter-specific competition and predation pressure may begin to influence population density at the new level, and become important in determining the long term carrying capacity of logged forest, but will be secondary to food availability.

Cords and Rowell (1987) state that the long inter birth interval in *C.mitis* (ca.47 months) would mean that they breed very slowly indeed. This may vary between sites and undergo a reduction in favourable conditions. Viewed in the long term, the period of 45 years since logging would be sufficient for population growth even if the longest possible inter-birth interval was observed in Budongo. It is interesting to note that recent group counts for three of the four study groups show increases in group size for both groups in logged forest, but one group in unlogged forest has remained approximately the same size (Chapter 4, A.Plumptre pers. comm.). There may also have been some immigration of monkeys (most likely immature males who also migrate under 'normal circumstances') from neighbouring compartments which form part of the contiguous forest block in Budongo and this would further contribute to population growth.

The long term demographic consequences of a higher population density are not fully understood and there may be changes occurring in parameters such as the birth rate, male tenure length and male-male competition as a result of the increase in density. Territoriality and competition levels may be higher in logged forest as indicated by the higher Index of Defendability and a higher relative density of other species : blue monkeys. In addition to differences in habitat and ecology, these factors will also be important in determining the long term population density of *C.mitis* in logged forest.

Logging in Budongo: some caveats

Based on the findings of this study, logging apparently results in an improved habitat and a subsequent increase in population density. There are several observations which must be made when incorporating these findings into a general context of understanding the effects of logging on primates and other wildlife. Most of these observations relate to the specific nature of the vegetation as well as the forest management which was carried out in Budongo forest. Some other observations relate to the ecological characteristics of the C.*mitis* group.

Firstly, it should be pointed out that unlogged areas of Budongo forest appear to tend towards *Cynometra* mono-dominance with an associated reduction in species diversity together with an increase in the proportion of tree species associated with this type of forest (Eggeling 1947a). In this context, logging disturbance may augment natural levels of disturbance and encourage re-growth which resembles colonising forest and has a higher tree species diversity and a higher proportion of colonising forest species. Even though mono-dominant forests may be more common in the tropics than previously thought (Connell and Lowman 1989, Hart 1990, 1995) the vegetation changes documented here will not be observed in all tropical forests which are scheduled for logging. In addition, not only is the overall forest type prior to logging in predicting responses, but individual tree species (exhibiting different growth strategies) will respond in different ways. Uhl et al (1993) in an effort to predict the responses of tree species to logging damage have developed a ranking system which scores for tree characteristics, geographic distribution and regeneration capacity. The use of such predictors may be useful tools for forest managers aiming to integrate biodiversity conservation and timber extraction.

Secondly, despite a heavy emphasis on silviculture and management aimed purely at timber production (Eggeling 1947b, Phillip and Beaton 1965, Treneman 1954), the felling system implemented by the Uganda Forest Department in Budongo was designed with some implicit sense of sustainability. This was 'sustainability' before the advent of tropical forest conservation and was couched largely in foresters terms, but the approach may have had some degree of 'ecological sustainability', even if more by accident than design.

Felling was carried out with the intention of causing minimum damage to residual stands and a long rotation system was being used. Regardless of the 'sustainability' of the management system, it was also tightly controlled and well documented at least until the late 1970's (Hamilton 1984). This at least meant that reasonably moderate and controlled levels of felling were undertaken throughout most of the logging history in Budongo. Post logging silviculture and management, which can improve the regeneration capacity of logged forest and minimise negative effects was also carried out. Interestingly, the widespread application of arboricide by the Forest Department in Budongo (Phillip and Beaton 1965) does not appear to have had a negative effect on overall species composition or the individual species singled out for treatment (e.g. Cynometra *alexandri* and several *Ficus* spp.). The system applied in Budongo was therefore very selective, carried out at a low intensity and well managed compared to other sites in the tropics.

The situation post-logging is also of great importance in determining the extent of change in the ecosystem, the regeneration capacity of logged forest and subsequently the ecological value of logged forest. Some aspects of management carried out in Budongo in the past were aimed at improving the abundance of desirable timber species (Eggeling 1947b, Philip 1965, Treneman 1954) which may not always have beneficial effects on wildlife and can often significantly alter the forest composition. Factors such as hunting and cultivation of secondary forest areas post logging are probably much more important than the direct effects of logging for the long term survival of forest areas (Buschbacher 1990, Fimbel 1994). In Budongo, there was negligible hunting pressure and very little agricultural encroachment, both critical for allowing wildlife populations to recover and forest regeneration to occur. Lawes (1992) states that samangos (*C.mitis erythrarchus*) in South Africa are threatened by forest disturbance of a much more intense nature where forest exploitation and loss of forest cover may considerably reduce the faunal carrying capacity of the forests. He emphasises the 'permanent removal of food resources' subsequent to logging and the heightened impact this may have on an ecosystem subject to seasonal shortages.

Finally, blue monkeys are most likely recent colonisers of forest areas, and it has been suggested that in their evolutionary past, they formerly inhabited open savannah woodland areas as semi-terrestrial frugivores (Leakey 1988). As a generalist species, the blue monkey may make use of gap edges and heavy liane growth both as areas of high food availability and resting sites. Skorupa (1986) observed that the ecological flexibility of *C.mitis* was one of the characteristics which allowed it to survive at unchanged densities in logged forest. This study has shown that blue monkeys in Budongo may even have benefited from logging and have certaily achieved higher population density as a direct result of the vegetation changes associated with logging.

Bearing in mind the implications of such results, it is vital to state that the results presented here may indicate the type of response expected from a frugivore primate which is largely seen as a dietary generalist. There are undoubtedly other more ecologically specialised taxa, which may not experience an increase in the quality of their habitat subsequent to logging (Weisenseel et al 1993, Skorupa 1986).

Logging and Conservation: a wider view

Before the results of this study are dismissed as being unrepresentative, it is worth pointing out that the changes in population density observed is not unique to blue monkeys, and the same flexibility may be observed in some other species/taxa. Among arboreal primates, ther is long standing evidence that generalist frugivores exhibit preferences for secondary forest (Fimbel 1994, Pinto et al 1993, Thomas 1991, Wilson and Wilson 1975) while those with a more specialised feeding niche or habitat requirements will select for primary forest. McGraw (1994) found *C.ascanius* and *C.wolfii* densities to be much lower in primary (monodominant) *Gilberteodendron* forest in Zaire. Thomas (1991) also found *C.mitis* , *C.ascanius* and *C.pogonias* showing a preference for secondary forest, using 'mbau' forest (*Gilberteodendron dewevrei* dominated) and 'mixed' forest (patchily occurring *Cynometra alexandri/ Brachystegia laurentii* dominated) less than expected. Fimbel (1994) showed a preference for secondary forest (agricultural re-growth) in 4 species of primate *C. campbelli, C. petaurista, Cerocebus atys* and *Pan troglodytes*. At Epulu, Eastern Zaire, Hart has found that densities of 12 out of 15 species are higher in disturbed forest as opposed to *Gilberteodendron* forest with the exception of *C.hamlynii,* which is an almost exclusively terrestrial species (A.Plumptre pers. comm.). The heterogeneity resulting from logging, if forest structure and cover is subsequently allowed to regenerate, may mean that there is considerable potential for conservation of forest primates in logged forest. Hamilton (1988), suggested that recent reductions in the extent of forest cover, together with a clarification of the forest/savannah boundary, may have influenced the ecological niche of some primates which were previously more wide-ranging between savannah and forest. Subsequent to the forest/savannah clarification, they may have become true forest dwelling monkeys, more arboreal in their habits and thus adaptations for forest life may be relatively recent.

The evidence for tolerance of habitat disturbance may also apply to other species/taxa with high ecological flexibility and indeed has been reported for birds (Johns 1991a, Thiollay 1992), mammals (Ganzhorn et al 1990, Kasenene 1984, Nummelin 1990, Nummelin and Borowiec1991), and invertebrates (Burghouts et al 1992). One key requirement is that disturbance levels should be as close to natural disturbance in scale and frequency (sensu Brown and Press 1992). In addition, consideration of this evidence should not overlook the negative effects of disturbance on some specialised or ecologically vulnerable species. The message is essentially that tolerance or preference for habitat disturbance indicates the potential for maintaining biodiversity in disturbed forests, given the appropriate level of disturbance. 'Disturbed', logged, or 'secondary' forests, are becoming an increasingly common habitat in the developing tropics as demands for timber extraction increase (Grieser Johns and Grieser Johns 1995) therefore it is important to recognise their potential value if managed carefully. Management and protection of logged forests may become an important part of integrated protected area management in many developing tropical nations.

Longer term effects

When addressing the long term sustainability of forest management, it is also important to consider the many unknown or hidden consequences of logging which may result. There may be unseen negative effects of changes in blue monkey population density, for diet and ranging patterns, which would not be apparent from this study. By narrowing its diet and feeding more frequently on fruit, the *C.mitis* population in logged forest may be more at risk during catastrophic food shortages due to it's inability to survive on a wider range of less profitable dietary items. There may be important consequences for inter-group interactions, male-male competition and diseases susceptibility at the new higher population density. For species with complex social organisation, the social disruption caused by logging may have severe negative effects (sensu White and Tutin unpubl. manuscript).

As far as vegetation changes are concerned, there is some concern amongst foresters and conservationists alike that continued felling of the best individuals of timber species will result in considerable long term 'genetic erosion' and lead to a decrease in quality of those species preferred as timber trees (Buschbacher 1990, Macedo and Anderson 1993, Uhl et al 1991). Burghouts et al (1992) discuss changes in tree species composition following logging which are likely to result in an increase in light demanding pioneer species and a decrease in shade bearing species. Pioneer species have a different pattern of leaf fall therefore different patterns of litter accumulation and soil conditions may be observed many years after logging. Congdon and Herbohn (1993) observed that 25 years after logging, nutrient concentrations were lower and soil densities were higher. Cannon et al (1994) discuss the need for an understanding of the long term effects of logging on seedling and sapling density. Kasenene (1984) reported an increase in species abundance and number of rodents in logged forest and concluded that as a result of seedling predation by these rodents, forest regenerative capacity and seedling survival would be negatively affected. These are only some of the examples of the type of effects occurring on a much longer time scale and potentially operating within and between communities. All of these factors will have some bearing on the overall sustainability of the system of management and should be considered wherever possible.

Implications for Forest Management in Uganda

Having discussed the theoretical implications of logging in the context of biodiversity conservation and the nature of the processes involved, it is now worth considering the real situation in Uganda for a final comment. As stated earlier, Ugandan forests are under great pressure to 'pay their way' and decisions regarding the fate of the remaining Forest Reserves are being taken at this moment (P. Howard pers. comm.). In an economic and political vacuum, where the only interests were in natural forest conservation, goals of forest management might be better achieved by maintaining a protected natural forest in Budongo and allowing the ecological transition to *Cynometra*--Mixed and *Cynometra* forest to take place. The level of disturbance which occurred naturally would maintain some species associated with colonising forest but this would probably result in a more 'natural' forest which ironically would be lower in overall diversity.

In reality however, the current political and economic situation in Uganda dictates that other factors will also be important in determining the management of Budongo Forest. It is apparent that a forest such as Budongo in a country like Uganda is under pressure to 'pay its way'. If selective logging can be carried out in a controlled and sustainable manner, then the economic potential of timber extraction may be realised without necessarily reducing the conservation value of the forest. Logged forests may serve as useful buffer areas as part of a larger protected area system as well as providing vital revenue for protection of remaining intact forests.

The observation that one species of arboreal primate actually increases in density, and that the results may be applicable to other species, suggests that selective logging and conservation do not have to conflict. This finding may encourage efforts from both foresters and conservationists to arrive at more suitable management strategies for acceptable logging.

One major problem remains in Budongo as far as integrating conservation and timber extraction is concerned: that is the lack of control of illegal logging and the threat this practice poses to the remaining forest. That pitsawying is both uncontrolled and detrimental to any form of forest management in Budongo is clear at present, and the negative effects of this drain on timber resources on future management potential is recognised by both foresters and conservationists in Uganda. The current level of timber extraction by illegal pitsawyers precludes any attempt by the Forest Department to assess the potential for sustainable management. In addition, it is a threat to the future value of the Budongo as a timber production and a conservation forest. This problem must be tackled, and attempts made to reinstate some form of sustainable management in Budongo. The key to meeting timber production and conservation goals relies on the appropriate intensity of felling and controlled, well planned management which minimises negative impacts on the forest ecosystem. Perhaps by being aware of this and carefully managing the inevitable logging, the conservation of bio-diversity can also be incorporated in Budongo's future management.

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APPENDICES

APPENDIX 1 Tree species list from vegetation plots (after Synott 1985)

Tree Species	*Family*	*N32*	*N151*	*Both*
1.*Argomuellera macrophylla*	??	+		
2.*Albizzia sp.*	LEGUMINOSAE/MIMOSOIDEAE	+	+	+
3.*Alchornea laxiflora*	EUPHORBIACEAE	+	+	+
4.*Allophyllus dummeri*	SAPINDACEAE	+	+	+
5.*Alstonia boonei*	APOCYNACEAE	+	+	+
6.*Aningeria altissima*	SAPOTACEAE	+	+	+
7.*Antiaris toxicaria*	MORACEAE	+	+	+
8.*Antidesma laciniatum*	EUPHORBIACEAE	+	+	+
9.*Apodytes dimidata*	ICACINACEAE	+	+	+
10.*Baphia wollastonii*	LEGUMINOSAE/PAPILIONIOIDEAE		+	
11.*Blighia unijugata*	SAPINDACEAE	+	+	+
12.*Blighia welwitschii*	SAPINDACEAE	+		
13.*Trilepsium madagascarensis*	MORACEAE	+	+	+
14.*Bridelia micrantha*	EUPHORBIACEAE	+		
15.*Bridelia sp.*	EUPHORBIACEAE	+		
16.*Caloncoba schweinfurthii*	FLACOURTACEAE	+	+	+
17.*Canarium schweinfurthii*	BURSERACEAE	+	+	+
18.*Celtis durandii*	ULMACEAE	+	+	+
19.*Celtis mildbraedii*	ULMACEAE	+	+	+
20.*Celtis wightii*	ULMACEAE	+	+	+
21.*Celtis zenkerii*	ULMACEAE	+	+	+
22.*Chrysophyllum albidum*	SAPOTACEAE	+	+	+
23.*Chrysophyllum muerense*	SAPOTACEAE	+	+	+
24.*Chrysophyllum perpulchrum*	SAPOTACEAE	+	+	+
25.*Cleistopholis patens*	ANNONACEAE	+		
26.*Coffea eugenoides*	RUBIACEAE	+	+	+
27.*Cola gigantea*	STERCULIACEAE	+		
28.*Corda milleni*	BORAGINACEAE	+	+	+
29.*Craibia brownii*	LEGUMINOSAE/PAPILIONIOIDEAE		+	
30.*Crossonephilis africana*	SAPINDACEAE	+	+	+
31.*Croton macrostachyus*	EUPHORBIACEAE	+	+	+
32.*Cynometra alexandri*	LEGUMINOSAE/CAESALPINIOIDEAE	+	+	+
33.*Desplatia dewevrei*	TILIACEAE	+	+	+
34.*Diospyros abyssinica*	EBENACEAE	+	+	+
35.*Entandrophragma angolense*	MELIACEAE	+	+	+
36.*Entandrophragma cylindricum*	MELIACEAE	+	+	+
37.*Entandrophragma utile*	MELIACEAE		+	
38.*Erythrophleum suaveolens*	LEGUMINOSAE/CAESALPINIOIDEAE	+	+	+
39.*Zanthoxylum leprieurii*	EUPHORBIACEAE	+		
40.*Fagaropsis angolense*	RUTACEAE	+		
41.*Ficus barterii*	MORACEAE		+	
42.*Ficus exasperata*	MORACEAE	+		
43.*Ficus lingua*	MORACEAE	+		
44.*Ficus mucoso*	MORACEAE	+		
45.*Ficus natalensis*	MORACEAE	+	+	+
46.*Ficus sansibarica*	MORACEAE	+		
47.*Ficus saussereana*	MORACEAE	+	+	
48.*Ficus sur*	MORACEAE	+	+	
49.*Ficus vallis-choudae*	MORACEAE	+		
50.*Ficus varifolia*	MORACEAE	+	+	+
51.*Funtumia africana*	APOCYNACEAE	+	+	+
52.*Funtumia elastica*	APOCYNACEAE	+	+	+

APPENDIX 1 (contd): Tree species list from vegetation plots (after Synott 1985)

Tree Species	*Family*	*N32*	*N151*	*Both*
53.*Guarea cedrata*	Meliaceae	+	+	+
54.*Holoptelea grandis*	Ulmaceae	+	+	+
55.*Khaya anthotheca*	Meliaceae	+	+	+
56.*Kigelia africana*	Bignoniaceae	+		
57.*Lannea welwitschii*	Anacardiaceae	+	+	+
58.*Lasciodiscus mildbraedii*	Rahmnaceae	+	+	+
59.*Leptonychia mildbraedii*	Sterculiaceae	+	+	+
60.*Lovoa trichiliodes*	Meliaceae		+	
61.*Lychnodiscus cerospermus*	Sapindaceae	+	+	+
62.*Maerua duchesnei*	Capparaceae		+	
63.*Maesopsis eminii*	Rhamnaceae	+	+	+
64.*Majidea fosterii*	Sapindaceae		+	
65.*Mallotus oppositifolius*	Euphorbiaceae	+		
66.*Mamea africana*	Guttiferae	+		
67.*Margaritaria discoidea*	Euphorbiaceae	+	+	+
68.*Markhamia lutea*	Bignoniaceae	+	+	+
69.*Melanodiscus oblongus*	??	+		
70.*Melicia excelsa*	Moraceae	+		
71.*Mildbraedeodendron excelsum*	Leguminosae/Caesalpinioideae	+	+	+
72.*Hallea stipulosa*	Rubiaceae	+		
73.*Monodora angolensis*	Annonaceae	+	+	+
74.*Monodora myristica*	Annonaceae		+	
75.*Morus lactea*	Moraceae	+	+	+
76.*Myrianthus arboreus*	Moraceae	+	+	+
77.*Ochna membrenacea*	Ochnaceae	+	+	+
78.*Olax gambicola*	??	+	+	+
79.*Olea welwitschii*	Oleaceae	+		
80.*Pancovia turbinata*	???	+		
81.*Paropsia guineensis*	Passifloraceae	+		
82.*Picralima nitida*	Apocynaceae		+	
83.*Pycnanthus angolensis*	Myristicaceae	+		
84.*Rauvolfia vomitoria*	Apocynaceae		+	
85.*Riciniodendron heudelotti*	Euphorbiaceae	+	+	+
86.*Rinorea beniensis*	Violoceae	+		
87.*Rinorea ilicifolia*	Violoceae	+	+	+
88.*Spathodea campanulata*	Bignoniaceae	+	+	+
89.*Strombosia scheffleri*	Olacaceae	+		
90.*Tabaernaemontana holstii*	Apocynaceae	+	+	+
91.*Tapura fischeri*	Dichapetalaceae	+	+	+
92.*Teclea noblis*	Rutaceae	+	+	+
93.*Tetrapleura tetraptera*	Leguminosae/Mimosoideae	+	+	+
94.*Tetrorchidium didymostemon*	Euphorbiaceae	+	+	+
95.*Trema orientalis*	Ulmaceae		+	
96.*Trichilia dregeana*	Meliaceae	+		
97.*Trichilia prieuriana*	Meliaceae	+	+	+
98.*Trichilia rubescens*	Meliaceae	+	+	
99.*Uvariodendron magnificum*	??		+	
100.*Uvariopsis congensis*	Annonaceae	+		
101.*Vitex doniana*	Verbenaceae	+	+	+

APPENDIX 1 (contd): Tree species list from vegetation plots

Tree Species	*Family*	*N32*	*N151*	*Both*
Unidentified Species				
102.N15.121.1			+	
103.N15.154.1			+	
104.N15.158.1			+	
105.N15.161.1			+	
106.N15.17.1			+	
107.N15.4.1			+	
108.N15.69.1			+	
109.N15.74.1			+	
110.N15.76.1			+	
111.N15.77.1			+	
112.N15.81.1			+	
113.N15.89.1			+	
114.N15.92.1			+	
115.N3.102,1		+		
116.N3.105.1		+		
117.N3.119.1		+		
118.N3.12.2		+		
119.N3.19.1		+		
120.N3.25.1		+		
121.N3.27.1		+		
122.N3.29.1		+		
123.N3.31.1		+		
124.N3.35.1		+		
125.N3.36.1		+		
126.N3.36.2		+		
127.N3.45.1		+		
128.N3.55.1		+		
129.N3.57.1		+		
130.N3.59.1		+		
131.N3.6.1		+		
132.N3.61.2		+		
133.N3.64.2		+		
134.N3.65.1		+		
135.N3.76.1		+		
136.N3.78.1		+		
137.N3.89.1		+		
138.N3.95.1		+		
139.N3.95.2		+		
140.N3.96.1		+		
141.N3.99.1		+		

APPENDIX 2. Dietary list for all four groups. (after Synott 1985)

		N3:Logged		N15:Unlogged	
Species	*Item*	N32	N31	N151	N152
Alafia landolphiodes	RF	*	*	*	*
Alafia landolphiodes	UF			*	
Alafia landolphiodes	LP			*	
Albizzia sp.	BA	*	*	*	*
Albizzia sp.	BU		*		
Albizzia sp.	FL	*	*		*
Albizzia sp.	ML	*			
Albizzia sp.	SE	*	*		
Albizzia sp.	SH				
Albizzia sp.	YL	*	*	*	*
Alstonia boonei	FL	*	*	*	*
Alstonia boonei	ML		*	*	*
Alstonia boonei	SE	*	*		
Alstonia boonei	SH	*	*	*	
Alstonia boonei	YL	*	*	*	*
Antiaris toxicaria	RF				*
Antiaris toxicaria	UF			*	*
Antiaris toxicaria	YL				*
Aphania senegalensis	RF				*
Aphania senegalensis	ML				*
Blighia unijugata	YL		*		
Bosqueia phoberos	BU	*	*	*	*
Trilepsium madagascarensis	FL	*		*	*
Trilepsium madagascarensis	RF	*		*	
Trilepsium madagascarensis	UF	*	*	*	*
Trilepsium madagascarensis	YL		*	*	*
Caloncoba schweinfurthii	BU		*		
Caloncoba schweinfurthii	FL	*	*		
Caloncoba schweinfurthii	RF				
Caloncoba schweinfurthii	UF	*		*	*
Caloncoba schweinfurthii	YL				
Canarium schweinfurthii	FL				
Canarium schweinfurthii.	YL				
Canarium scweinfurthii.	RF			*	
Celtis durandii	BU	*	*	*	*
Celtis durandii	FL	*			
Celtis durandii	ML				*
Celtis durandii	RF	*	*	*	*
Celtis durandii	UF	*	*	*	*
Celtis durandii	YL	*	*		
Celtis mildbraedii	BU	*	*	*	*
Celtis mildbraedii	FL			*	*
Celtis mildbraedii	ML	*	*	*	*
Celtis mildbraedii	RF	*		*	
Celtis mildbraedii	UF	*		*	*
Celtis mildbraedii	YL	*	*	*	*
Celtis wightii	BU		*		
Celtis wightii	RF		*		
Celtis wightii	YL			*	
Celtis zenkerii	BU	*	*	*	*
Celtis zenkerii	FL			*	*
Celtis zenkerii	ML	*	*	*	
Celtis zenkerii	RF	*	*	*	*

APPENDIX 2 (contd.): Dietary list for all four groups

			N3:Logged		N15:Unlogged	
Species	*Item*		*N32*	*N31*	*N151*	*N152*
Celtis zenkerii	UF		*	*	*	*
Celtis zenkerii	YL		*	*	*	*
Chrysophllyum albidum.	FL		*	*	*	
Chrysophllyum albidum	RF		*	*	*	
Chrysophllyum albidum	UF		*	*	*	
Chrysophyllum albidum	BU			*		
Chrysophyllum albidum	FL					
Chrysophyllum perpulchrum.	BU			*		
Chrysophyllum perpulchrum.	FL			*	*	*
Chrysophyllum perpulchrum.	RF			*		*
Chrysophyllum perpulchrum	UF			*	*	*
Chrysophyllum perpulchrum.	YL					
Cleistopholis patens	BU			*		*
Cleistopholis patens	RF		*	*	*	
Cleistopholis patens	UF		*	*	*	*
Cleistopholis patens	YL		*			
Coffea eugenoides	RF			*		*
Coffea eugenoides	YL				*	
Cordia milleni	BU		*	*	*	
Cordia milleni	FL		*	*		*
Cordia millenii	RF					*
Cordia milleni	UF		*	*	*	*
Cordia milleni	YL		*	*		
Crossonephilis africanana	FL				*	
Crossonephilis africanana	SE			*		
Crossonephilis africanana	UF			*		
Crossonephilis africanana	YL			*		
Croton macrostachyus	BU			*	*	
Croton macrostachyus	FL		*	*		
Croton macrostachyus	RF		*	*	*	
Croton macrostachyus	UF		*	*		
Cynometra alexandri	BU			*	*	*
Cynometra alexandri	FL		*	*	*	*
Cynometra alexandri	ML				*	*
Cynometra alexandri	SE			*	*	*
Cynometra alexandri	YL		*	*	*	*
Desplatsia dewevrei	FL		*	*		
Desplatsia dewevrei	RF			*		
Desplatsia dewevrei	YL		*			
Diospyros abyssinica	ML					
Diospyros abyssinica	RF					*
Diospyros abyssinica	UF			*		*
Diospyros abyssinica	YL			*		
Entandrophragma spp.	BA					*
Entandrophragma spp.	FL				*	*
Entandrophragma spp.	UF				*	*
Erythrophleum suaveol	FL				*	*
Erythrophleum suaveol.	SE					
Erythrophleum suaveol.	YL				*	*
Zanthoxylum leprieurii	RF					*
Zanthoxylum leprieurii	ML					*
Ficus asperifolia	RF					*
Ficus barterii	BU			*		
Ficus barterii	YL		*			
Ficus exasperata	BU	*	*			
Ficus exasperata	RF	*	*			

APPENDIX 2 (contd.): Dietary list for all four groups

		N3:Logged		*N15:Unlogged*	
Species	*Item*	*N32*	*N31*	*N151*	*N152*
Ficus exasperata	UF	*	*		
Ficus exasperata	YL	*			
Ficus lingua	BU	*			*
Ficus lingua	FL			*	
Ficus lingua	RF		*	*	*
Ficus lingua	UF				*
Ficus lingua	YL	*			
Ficus natalensis	RF	*			*
Ficus natalensis	UF	*			
Ficus polita	RF		*		
Ficus sansibarica	BU	*			
Ficus sansibarica	RF	*	*		
Ficus sansibarica	UF	*			
Ficus sansibarica	YL	*			
Ficus sp.	BU			*	
Ficus sp.	ML				*
Ficus sp.	UF				*
Ficus sp.	YL			*	
Ficus sur	BU	*	*		
Ficus sur	RF	*			
Ficus sur	UF	*	*	*	
Ficus sur	YL	*			
Ficus vallis-choudae	RF	*			
Ficus varifolia	RF	*			
Ficus varifolia	BU	*			
Funtumia elastica	FL			*	
Funtumia elastica	SE	*	*	*	*
Funumia elastica	SH	*			
Guarea cedrata	SE		*	*	
Guarea cedrata	YL				
Holoptelea grandis	BU		*	*	*
Holoptelea grandis	YL			*	
Iodes africana	RF		*	*	
Khaya anthotheca	BA	*	*	*	*
Khaya anthotheca	FL	*			*
Khaya anthotheca	ML		*		
Khaya anthotheca	YL	*		*	
Klainedoxa gabonensis	RF			*	
Lasciodiscus mildbraedii	FL			*	*
Lasciodiscus mildbraedii	ML			*	
Lasciodiscus mildbraedii	SE	*	*		
Loranthus sp.	RF	*			
Loranthus sp.	BU	*			
Lychnodiscus cerospermus	SE				*
Maesopsis eminii	BA				
Maesopsis eminii	BU		*		
Maesopsis eminii	FL			*	
Maesopsis eminii	RF	*	*	*	*
Maesopsis eminii	UF	*	*	*	*
Maesopsis eminii	YL	*	*		
Mallotus oppositifolius	BU		*		
Margariaria discoides	BU	*	*		
Margariaria discoides	RF	*	*	*	*
Margariaria discoides	UF	*	*	*	*
Mildbraedeodendron excelsum	FL			*	*
Mildbraedeodendron excelsum	RF			*	*

APPENDIX 2 (contd.): Dietary list for all four groups

		N3:Logged		*N15:Unlogged*	
Species	*Item*	*N32*	*N31*	*N151*	*N152*
Mildbraedeodendron excelsum	YL			*	
Milicia excelsa	BU				*
Monodora myristica	YL		*		
Morus lactea	ML			*	
Morus lactea	RF		*	*	*
Morus lactea	UF		*	*	*
Myrianthus arboreus	RF			*	
Myrianthus arboreus	UF			*	
Olea welwitschii	UF		*		
Paropsia guineensis	RF				*
Paropsia guineensis	ML				*
Piper guineense	RF				*
Psidium guava	YL		*		
Psidium guava	RF		*		
Ressantia parvifolia	FL				*
Ressantia parvifolia	SE	*			
Ressantia parvifolia	YL				
Ricinodendron heudelelotti	UF			*	
Rinorea ilicifolia	RF			*	
Strychnos mitis	BU		*		
Strychnos mitis	YL				*
Strychnos mitis	ML		*		
Tapura fischerii	UF				*
Teclea noblis	RF				*
Tetrachidium didymostemum	UF	*			*
Tetrapleura tetraptera	SE	*			
Trichilia prieuriana	FL		*		*
Trichilia prieuriana	RF		*	*	*
Turraeanthus africanus	FL		*		

APPENDIX 3 Selection Ratios (SR) for the top five food items in each two day follow.

Item Codes: ML=Mature Leaves, YL=YoungLeaves, BU=Leaf Buds, UF=Unripe Fruit, RF=Ripe Fruit, Fl=Flowers, LP=Leaf Petiole, BA=Bark, SE=Seeds.

	N151			*N32*		
	Species	*Item*	*SR*	*Species*	*Item*	*SR*
Jul-01 (1993)	*Celtis mildbraedii*	YL	9.03	*Cynometra alexandri*	YL	1.57
	Cynometra alexandri	YL	0.74	*Celtis durandii*	RF	5.62
	Unidentified	UF		*Alstonia boonei*	LP	0.93
	Chrysophyllum albidum	FL	5.48	*Cordia millenii*	UF	11.8
	Mildbradeodendron excelsum	RF	14	*Chrysophyllum albidum*	FL	3.6
Jul-02	*no data*			*Celtis durandii*	UF	1
				Bosqueia phoberos	BU	
				Cynometra alexandri	YL	1.5
				Alstonia boonei	YL	0.63
				Ficus lingua	BU	
Aug-01	*Cynometra alexandri*	YL	0.74	*no data*		
	Celtis mildbraedii	YL	2.92			
	Celtis durandii	UF	2.5			
	Margaritaria discoides	UF	19.2			
	Mildbraedeodendron exc.	RF	12.3			
Aug-02	*Celtis durandii*	RF	7.02	*Celtis durandii*	RF	1.25
	Cynometra alexandri	FL	1.78	*Ficus sur*	BU	0.8
	Celtis mildbraedii	YL	1.28	*Ficus sur*	RF	3.85
	Cynometra alexandri	YL	0.21	*Albizzia sp.*	BA	1.36
	Mildbradeodendron excelsum	RF	22.4	*Croton macrostachyus*	RF	2.23
Sep-01	*Celtis durandii*	RF	29.1	*Celtis durandii*	RF	1.24
	Cynometra alexandri	YL	0.32	*Croton macrostachyus*	UF	5.95
	Celtis mildbraedii	YL	1.33	*Ficus sur*	YL	2.09
	Cynometra alexandri	FL	1.5	*Celtis zenkerii*	RF	2.42
	Celtis zenkerii	RF	16.1	*Celtis zenkerii*	UF	1.41
Sep-02	*Celtis durandii*	RF	27.4	*Celtis durandii*	RF	0.9
	Celtis zenkerii	RF	26.1	*Cynometra alexandri*	YL	2.82
	Cynometra alexandri	FL	0.69	*Celtis mildbraedii*	YL	2.18
	Croton macrostacyhus	RF	4.37	*Margaritaria disciode*	RF	31.5
	Celtis mildbraedii	BU	5.66	*Croton macrostachyus*	RF	4.57
Oct-01	*Celtis durandii*	RF	5.24	*Celtis durandii*	RF	1.69
	Celtis mildbraedii	YL	1.29	*Celtis zenkerii*	RF	6.91
	Cynometra alexandri	YL	0.26	*Ficus sur*	RF	7.5
	Celtis zenkerii	RF	14.9	*Ficus sur*	UF	0.71
	Cynometra alexandri	FL	1.17	*Ficus sur*	YL	0.7
Oct-02	*Celtis durandii*	RF	12.8	*Celtis durandii*	RF	1.88
	Celtis zenkerii	RF	25.6	*Cynometra alexandri*	YL	0.3
	Cynometra alexandri	FL	1.78	*Celtis mildbraedii*	YL	0.56
	Celtis mildbraedii	BU	3.03	*Ficus sur*	RF	0.83
	Cynometra alexandri	YL	0.03	*Coffea eugenoides*	SE	26.7

APPENDIX 3 (contd.): Selection Ratios (SR) for the top five food items in each two day follow.

Item Codes: ML=Mature Leaves, YL=YoungLeaves, BU=Leaf Buds, UF=Unripe Fruit, RF=Ripe Fruit, Fl=Flowers, LP=Leaf Petiole, BA=Bark, SE=Seeds.

Nov-01	*Cynometra alexandri*	*YL*	*0.32*	*Celtis durandii*	*RF*	*1.83*
	Celtis durandii	*RF*	*14.9*	*Celtis zenkerii*	*RF*	*12.2*
	Celtis mildbraedii	*YL*	*1.16*	*Ficus sur*	*RF*	*5.52*
	Celtis zenkerii	*RF*	*5.28*	*Ficus sur*	*UF*	*0.99*
	Riciniodendron heudel.	*SE*	*3.3*	*Margaritaria disciode*	*RF*	*25.5*
Nov-02	*Celtis zenkerii*	*RF*	*28*	*Celtis durandii*	*RF*	*3.14*
	Celtis durandii	*RF*	*16.1*	*Cynometra alexandri*	*YL*	*0.44*
	Celtis mildbraedii	*BU*	*12*	*Ficus sur*	*RF*	*4.93*
	Cynometra alexandri	*FL*	*1.24*	*Ficus sur*	*UF*	*3.7*
	Ficus sp.	*YL*	*24.4*	*Celtis zenkerii*	*RF*	*5.09*
Dec-01	*Celtis mildbraedii*	*YL*	*1.46*	*Celtis durandii*	*RF*	*7.69*
	Cynometra alexandri	*YL*	*0.27*	*Ficus sur*	*BU*	*3.25*
	Celtis durandii	*RF*	*17.7*	*Celtis zenkerii*	*RF*	*3.39*
	Celtis zenkerii	*RF*	*6.4*	*Celtis mildbraedii*	*UF*	*14.8*
	Cleistopholis patens	*RF*	*6.77*	*Cleistopholis patens*	*RF*	*4.49*
Dec-02	*Celtis durandii*	*RF*	*121*	*Celtis durandii*	*RF*	*5.12*
	Trilepsium madagascare.	*RF*	*69.7*	*Ficus sur*	*UF*	*1.56*
	Mildbradeodendron excel.	*YL*	*5.65*	*Ficus sur*	*BU*	*2.56*
	Cynometra alexandri	*YL*	*0.12*	*Cynometra alexandri*	*YL*	*0.15*
	Unidentified	*RF*	*60*	*Celtis mildbraedii*	*YL*	*0.49*
Jan-01 *(1994)*	*Celtis durandii*	*RF*	*6.72*	*Celtis mildbraedii*	*YL*	*1.63*
	Celtis mildbraedii	*YL*	*1.08*	*Ficus sur*	*UF*	*1.47*
	Alstonia boonei	*FL*	*2.2*	*Ficus exasperata*	*UF*	*3.03*
	Cynometra alexandri	*YL*	*0.44*	*Celtis durandii*	*RF*	*4.61*
	Entandrophragma cylind.	*SE*	*19.8*	*Cynometra alexandri*	*YL*	*0.41*
Jan-02	*Chrysophyllum albidum*	*RF*	*187*	*Ficus exasperata*	*RF*	*4.94*
	Entandrophragma cylind.	*FL*	*7.02*	*Alstonia boonei*	*SE*	*1.68*
	Unidentified	*BU*	*90.9*	*Ficus exasperata*	*UF*	*4.3*
	Funtumia elastica	*SE*	*10.6*	*Ficus sur*	*RF*	*18.2*
	Holoptelea grandis	*BU*	*5.53*	*Ficus sur*	*UF*	*1.27*
Feb-01	*Chrysophyllum albidum*	*RF*	*28.4*	*Ficus sur*	*RF*	*3.48*
	Cynometra alexandri	*SE*	*1.57*	*Ficus exasperata*	*RF*	*7.27*
	Celtis mildbraedii	*YL*	*0.75*	*Cynometra alexandri*	*YL*	*1.05*
	Maesopsis eminii	*UF*	*0.51*	*Ficus exasperata*	*UF*	*4.73*
	Alafia landolphioides	*RF*	*54.1*	*Celtis durandii*	*BU*	*1.57*
Feb-02	*Maesopsis eminii*	*RF*	*8.92*	*Maesopsis eminii*	*RF*	*4.76*
	Morus lactea	*RF*	*47.7*	*Ficus sur*	*UF*	*3.15*
	Chrysophyllum albidum	*RF*	*12.2*	*Ficus sur*	*RF*	*1.51*
	Cynometra alexandri	*SE*	*0.47*	*Chrysophyllum albidum*	*RF*	*13.2*
	Morus lactea	*ML*	*3.05*	*Ficus exasperata*	*RF*	*16.4*
Mar-01	*Maesopsis eminii*	*RF*	*73.2*	*Maesopsis eminii*	*UF*	*13.2*
	Cynometra alexandri	*SE*	*1.78*	*Maesopsis eminii*	*RF*	*3.3*
	Holoptelea grandis	*BU*	*5.81*	*Albizzia sp.*	*FL*	*2.66*
	Cynometra alexandri	*YL*	*0.28*	*Ficus sur*	*UF*	*3.36*
	Chrysophyllum albi.	*RF*	*13.3*	*Celtis mildbraedii*	*YL*	*0.68*

APPENDIX 3 (contd.): Selection Ratios (SR) for the top five food items in each two day follow.

Item Codes: ML=Mature Leaves, YL=YoungLeaves, BU=Leaf Buds, UF=Unripe Fruit, RF=Ripe Fruit, Fl=Flowers, LP=Leaf Petiole, BA=Bark, SE=Seeds.

Mar-02	*Cynometra alexandri*	FL	11.3	*Maesopsis eminii*	RF	15
	Maesopsis eminii	RF	15.7	*Ficus sur*	RF	4.48
	Cynometra alexandri	YL	0.48	*Ficus exasperata*	UF	2.24
	Chrysophyllum albidum	RF	52.9	*Chrysophyllum albidum*	RF	32
	Celtis zenkerii	BU	0.35	*Ficus exasperata*	RF	7.24
Apr-01	*Maesopsis eminii*	RF	35.3	*Maesopsis eminii*	RF	15.2
	Iodes africana	RF	86.3	*Ficus exasperata*	UF	17.3
	Celtis zenkerii	BU	0.27	*Celtis mildbraedii*	YL	0.9
	Celtis mildbraedii	YL	0.47	*Celtis durandii*	YL	2.52
	Cynometra alexandri	YL	0.11	*Cynometra alexandri*	YL	0.19
Apr-02	*Maesopsis eminii*	RF	37.9	*Maesopsis eminii*	RF	25.2
	Celtis mildbraedii	BU	23.7	*Ficus exasperata*	UF	2.77
	Celtis zenkerii	FL	0.71	*Ficus sur*	RF	0.53
	Celtis mildbraedii	UF	21.9	*Ficus exasperata*	RF	1.73
	Alstonia boonei	LP	6.15	*Ficus sur*	UF	0.35
May-01	*Maesopsis eminii*	RF	37	*Maesopsis eminii*	RF	81.4
	Celtis mildbraedii	YL	5.48	*Ficus sur*	UF	2.67
	Celtis zenkerii	UF	0.48	*Ficus exasperata*	RF	11.5
	Entandrophragma cylind.	SE	1.47	*Ficus sur*	RF	0.8
	Funtumia elastica	SE	1.19	*Cynometra alexandri*	YL	0.31
May-02	*Maesopsis eminii*	RF	201	*Ficus sur*	RF	22.7
	Celtis mildbraedii	BU	31.9	*Celtis mildbraedii*	YL	2.34
	Guarea cedrata	RF	10.1	*Cynometra alexandri*	YL	0.72
	Myrianthus arboreus	RF	12.3	*Ficus exasperata*	RF	14.9
	Celtis durandii	RF	0.8	*Khaya anthotheca*	BA	1.53
Jun-01	*Cynometra alexandri*	YL	1.56	*Ficus sur*	RF	3.78
	Celtis mildbraedii	YL	2.84	*Ficus sur*	UF	1.97
	Funtumia elastica	SE	6.74	*Celtis mildbraedii*	BU	1.52
	Maesopsis eminii	RF	52.8	*Khaya anthotheca*	BA	5.16
	Celtis durandii	UF	1.79	*Ficus exasperata*	RF	16
Jun-02				*Celtis durandii*	UF	0.74
				Ficus sur	RF	2.1
				Cynometra alexandri	YL	1.1
				Khaya anthotheca	BA	2.39
				Croton macrostachyus	FL	6.47

APPENDIX 4 Publication

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Brief Report

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Infanticide and Infant Eating in the Blue Monkey *(Cercopithecus mitis stuhlmanni)* in the Budongo Forest Reserve, Uganda

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Key Words
Infanticide • Guenons • *Cercopithecus mitis* • Meat eating • Blue monkey • Field study • Budongo Forest Reserve

Infanticide by adult males in non-human primates was first observed by Sugiyama [1] in grey langurs and has since been documented for many other species including: *Cercopithecus mitis*, *C. ascanius* [2–4]; *Alouatta palliata*, *A. seniculus* [5, 6], and *Colobus badius* [3]. Several hypotheses have been suggested to explain infanticide [for a review, see 7], but testing such hypotheses is difficult given the patchiness of data. Infanticide is also rarely directly observed in the field and is often only inferred from attempted attacks by the male or strongly suspected following the disappearance of the infant. Observations are therefore important in generating further data for testing hypotheses. Here, I document a case of observed infanticide and subsequent eating of the infant by an adult male blue monkey shortly after his take-over of a group. Although infanticide has previously been recorded for blue monkeys [2], this is the first record of infant eating.

Observations took place in the Budongo Forest Reserve, Uganda, during an ongoing study of the comparative ecology of blue monkeys in areas of logged and unlogged forest. The Budongo Forest Reserve is a 420 km^2 area of semideciduous rain forest in Western Uganda [for details, see 8]. This study took place from January 1993 to August 1994 and involved data collection from 4 habituated groups of blue monkeys on a bimonthly basis. Previous studies of blue monkeys have consistently revealed a one-male group structure [9], and their diet is largely frugivorous, supplemented with leaves, flowers and insects. The average home range size of the 4 study groups is estimated at approximately 10 ha. Group N32, the group in which the infanticide took place, consisted of 10 individuals: 1 adult male and 4 adult females along with 2 immature and 3 juvenile offspring of those females.

During a dawn-to-dusk follow of group N32 on 15th September 1993, I observed that the adult male in the group had been replaced by a new male. The exact date of the take-over is not known, but must have taken place since the previous dawn-to-dusk follow, 21 days earlier (25th August 1993). The new male was easily recognisable from a wound near the tip of his tail, his larger body size and by his 'pyow' call [10]. The previous male had been present in the group for at least 6 months, since January 1993. I also recorded the presence of a new infant in the group during the dawn-to-dusk follow of 15th September. This infant must also have been born between 25th August and 15th September 1993, so it was not more than 3 weeks old.

The following day (16th September), during a dawn-to-dusk follow, I observed the new male kill and subsequently eat the infant as described below.

At 9.15 h, sounds of a chase were heard in the mid-canopy (20–30 m), and the adult male was seen chasing a female carrying an infant. The chase continued into thick cover, where I lost sight of the individuals; but soon afterwards I heard an object fall approximately 25 m to the ground. After hearing 'trill' distress calls [10] and looking for the source, I realised that the infant was on the ground, and although still alive, may have been injured. At 9.20 h, in response to the calls of the infant, 2 females (one of them the mother) descended to the low canopy (0–10 m) and scanned the undergrowth, apparently looking for the infant. Immediately after this, the male also descended to the low canopy, chased the females back up into the higher canopy and remained at a height of around 5 m, calling ('ka-train' [10]) and scanning the undergrowth. At 9.25 h, after apparently having seen the infant, the male descended to the ground (still calling), moved directly to where the infant was and picked it up in his mouth. He then climbed back into the under storey and moved to a height of approximately 10 m. He paused at this height and delivered a bite to the head of the infant while holding it by the forearms. The mother of the infant then gave a brief chase during which the male evaded her and carried the dead infant approximately 30 m away into the low canopy (around 15 m) of a *Cynometra alexandri* tree. He began to eat the infant at 9.33 h, removing and eating the intestines followed by the flesh from the ribs and the spine. The skull was then cracked open and the brain eaten, followed by the flesh from the forelimbs and shoulders. The male continued feeding on the rest of the carcass until 10.25 h, when he dropped the remains and moved off to join the group.

During the time the male was consuming the infant, the rest of the group at first remained sitting very quietly within a radius of approximately 20–30 m. They made no attempt to approach the male. Then, at about 10.12 h, some of the group members started moving and feeding as normal.

Events Following Infanticide

For 4 days following the infanticide, group N32 was followed by myself and Geresomu Muhumuza for a total of 20 observation hours, with efforts being made to follow the adult male and record any interactions between him and the rest of the group members. During these 20 h of observations, the male was seen to copulate with 3 of the 4 adult females but not with the mother of the dead infant. Some of these copulations were solicited by females following the male, grooming him and presenting their hindquarters. Juveniles avoided the male by remaining some distance away and fleeing whenever he approached. The male was also seen chasing an immature male on 2 occasions.

Further observations also took place during dawn-to-dusk follows until the end of the study (20th September 1994) and the male was seen copulating with the mother of the dead infant approximately 3–4 weeks after the infanticide. In addition, a new infant was recorded in the group on the 23rd November 1993. The male did not show any signs of aggression towards either the mother or the infant up to the end of the study period.

This observed case of infanticide and infant eating by an adult male blue monkey, together with other previous records [2, 3], suggests that infanticide may be a common occurrence. Although infanticide has previously been recorded for blue monkeys, this is the first case where the adult was subsequently observed to eat the dead infant. Although these observations alone cannot lead directly to a test of hypotheses, several lines of evidence tend to support the sexual selection hypothesis [11]. Firstly, the new infant almost certainly was not fathered by the new male, since the old male was present in the group for at least 6 months and the gestation period is approximately 4–5 months [1, 12]. The infant was also still being suckled, so the lactating female was not in breeding condition. Finally, the new male successfully copulated with the mother of the dead infant (as well as with other females), and is therefore likely to have increased his reproductive success (also dependent on his tenure length, which is not known but was at least 12 months).

Interestingly, the male did not show any signs of aggression to the infant born into the group on the 23rd November. This infant is highly likely to have been fathered by the previous male, but the female strategy of soliciting copulation with the new male may have been successful in 'cuckolding' him.

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Announcement

11th Annual Meeting of the Italian Association of Primatology
September 28–30, 1995, Pistoia, Italy

Thursday, September 28

14.00 h	Registration
15.00 h	Opening Lecture: Ape, Man, Apeman from Prehistoric to Modern Times Prof. G. Giacobini, University of Turin
16.30–18.30 h	Scientific Session 1: Primate Management
21.00 h	Welcome Concert

Friday, September 29

09.00–12.00 h	Scientific Session 2: Primate Biology
14.00–17.00 h	Scientific Session 3: Primate Behaviour
17.30 h	General Assembly of the 'Associazione Primatologica Italiana'
20.30 h	Social Dinner

Saturday, September 30

09.00–12.00 h	Round Table: Confiscated Chimpanzees in Italy: What to Do

Pistoia is a quiet, medium-sized town, Roman in origin, richly supplied with monuments dating both from the medieval and the Renaissance periods. Pistoia can be easily reached by train or coach from Florence (20 km). All Scientific Sessions will be held in the old Bishop's Palace situated on the Piazza Del Duomo.

Registration is free of charge; abstracts will be published in *Folia Primatologica*.

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Abstracts, Part 1

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Abstracts from the
6th Scientific Meeting of the Société Francophone de Primatologie

Held at Université Montpellier II, October 13–14, 1994

Translated by Prof. *B.L. Deputte*

1/1

Long-Term Survey of a Population of Sifakas *(Propithecus verreauxi coquereli)* in Ankarafantsika Forest (North-West Madagascar)

Suivi d'une population de *Propithecus verreauxi coquereli* dans le nord-ouest de Madagascar (massif forestier de l'Ankarafantsika)

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A population of sifakas *(Propithecus verreauxi coquereli)* has been surveyed repeatedly during 16 years (1978–1994) in Ankarafantsika forest reserve. This paper reports changes observed in this population during this period. Initially, it consisted of 38 individuals, divided into eight family groups, six living in primary deciduous forest and two in forest within an agricultural area. All individuals were marked. After 16 years, the sifaka groups living in the primary forest had changed little, either in size (net increase = 12.5%) or in range. In contrast, in the habitat influenced by humans, the sifaka groups showed a significant increase in size (net increase = 64%), associated with the formation of two new groups, and marked changes in their use of the environment.

1/2

Dispersion in *Callithrix jacchus* (Callitrichidae, Primates) at Nisia Floresta, North-East Brazil

Dispersion chez le *Callithrix jacchus* (Callitrichidae, Primates) à Nisia Floresta, dans le Nord-Ouest du Brésil

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The mating systems of the different species within the family Callitrichidae are very variable. However, studies of dispersion of these New World primates are scarce. This study reports on dispersion in two groups of *Callithrix jacchus*. One of the groups, PL, occupied an area of an experimental plantation of eucalyptus (*Eucalyptus* spp.), mahogany *(Swietenia macrophylla)* and several species of fruit tree. Throughout the study period, this group included 2 reproductive females and 1 reproductive