Behavioural Ecology of Duikers (Cephalophus spp.) in Forest and Secondary Growth, Taï, Côte d'Ivoire.

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Abstract

The behavioural ecology of duikers (*Cephalophus* spp.) was studied in mature forest and mixed secondary vegetation around Taï National Park, Côte d'Ivoire. The most common species in both vegetation types was *C. maxwelli*, followed by *C. dorsalis*, *C. ogilbyi*, *C. niger*, *C. zebra* and *C. jentinki* in mature forest, and *C. niger*, *C. dorsalis* and *C. sylvicultor* in secondary vegetation. Population surveys were carried out by a number of methods. Transect censuses by night were found most efficient in mature forest, whereas in secondary vegetation, only pellet transect censuses and drives into nets were possible. *C. maxwelli* populations were estimated at about 63 km^{-2} in mature forest and 79 km^{-2} in secondary vegetation.

Duikers were primarily frugivorous, but the proportion of leaves taken increased in the season of fruit scarcity. Fruit abundance in different habitats increased with the age of the vegetation.

Six *C. maxwelli* in mature forest and four in secondary vegetation were radio-collared to determine ranging patterns and social behaviour. They were diurnal and lived in groups of one male with one or two females and young. Home ranges, which were about 5 ha in size in mature forest and 3.6 ha in secondary vegetation, were defended by males, and the boundaries were marked by latrine areas by both sexes. In mixed secondary vegetation, all habitats were used except open fields and bamboo thickets.

Implications for conservation and management are discussed. The continued preservation of mature forest and the control of poaching are essential for the survival of the three rarer species (*C. jentinki*, *C. zebra* and *C. ogilbyi*). The control of poaching must precede any programme of sustainable harvesting of the more abundant species, which could be carried out in secondary vegetation. Duiker farming may be possible if low-cost sources of fencing and forage can be identified.

Resumé

Une étude a été faite de l'écologie et l'organisation sociale des céphalophes (Cephalophus spp.) en forêt primaire et en végétation secondaire d'âge divers aux alentours du Parc National de Taï, Côte d'Ivoire. L'éspèce la plus abondante dans les deux types de végétation était C. maxwelli, avec C. dorsalis, C. ogilbyi, C. niger, C. zebra et C. jentinki en forêt primaire et C. niger, C. dorsalis et C. sylvicultor en végétation secondaire. Une varieté de méthodes a été utilisée pour le recensement des populations. Le comptage d'animaux par contacts visuels pendant la nuit était la méthode la plus efficace en forêt primaire, mais seulement deux méthodes étaient possibles en végétation secondaire, c'est à dire le comptage de crottes et le capture au filet. Les densités estimées de C. maxwelli étaient 63 km^{-2} en forêt primaire et 79 km^{-2} en végétation secondaire.

Le régime alimentaire des céphalophes était basé sur les fruits, mais la proportion de feuilles augmentait à l'époque de rareté de fruits. L'abondance de fruits dans les différents habitats augmentait avec l'âge de la végétation.

On a mis des colliers-radio sur six C. maxwelli en forêt primaire et quatre en végétation secondaire, afin de détérminer leurs domaines vitaux et leur organisation sociale. Les C. maxwelli étaient diurnes et ils vivaient en petits groups d'un mâle avec une ou deux femelles et ses enfants. Les domaines vitaux étaient d'une taille d'environ 5 ha en forêt primaire et 3.6 ha en végétation secondaire. Les mâles défendaient leurs domaines contres les autres et les deux sexes marquaient les limites des domaines par moyen de laissées de fèces. Dans végétation secondaire, les C. maxwelli utilisaient tous les habitats sauf les champs et les forêts de bambou.

La préservation de la forêt primaire et le règlement de la chasse sont essentiels à la survie des trois espèces les plus rares (C. jentinki, C. zebra et C. ogilbyi). Le règlement de la chasse doit précéder aucune programme d'utilisation soutenable des céphalophes. L'élévage des céphalophes pour la production de la viande serait peut-être viable si on pouvait identifier des matériaux économiques pour la construction des enclos et pour l'alimentation des animaux.

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CHAPTER 1. INTRODUCTION

1.1. Reasons for the study

The rain forests of West Africa originally covered an area of about 680 000 km^2, but 80% are already gone, converted by agriculture and logging into secondary thickets, farms and plantations (Martin, 1991). At 2 900 km^2 a year, Côte d'Ivoire has one of the highest rates of deforestation of any country in the world (FAO, 1988), and of its original 140 000 km^2 of rain forest, only 30 000 km^2 remain. A further 30 000 km^2 are covered in coffee and cocoa plantations; 10 000 km^2 in food crops, and 70 000 km^2 in secondary vegetation on areas of forest fallow (Martin, 1991). Left to itself, much of this thick secondary growth (locally known as "farmbush") would eventually revert to forest, but given the ever-increasing pressure for land which results in shortened fallow periods, farmbush has become the predominant vegetation form in much of the forest belt of West Africa. What resources does this newly spreading habitat offer to the forest fauna? Which species will be able to adapt outside the forest remnants? Even if they can adapt to the change in vegetation, will they be able to survive the ever-increasing pressure of hunting?

Duikers are an important group to study in this respect for two reasons. Firstly, the large number of sympatric congenerics (seven species of Cephalophus in Taï National Park) suggests a fine separation of ecological niches. It is likely that some species are more adaptable to habitat disturbance than others. Only when this is understood can we plan the necessary conservation measures for the more vulnerable species.

Secondly, bushmeat is the most important source of meat for local people throughout forested West Africa, and duikers and monkeys are the most common prey species (Davies, 1987; S. Lahm, 1991; personal observation). In the forest belt of Côte d'Ivoire the meat consumption per person for the year of 1979 was 12.5 kg of bushmeat and 12 kg of fish, compared with just 3.4 kg of domestic animals (Adou, 1991). Are duikers being driven towards extinction by habitat destruction and hunting, or could they be managed for food production, either by the introduction of hunting quotas, or through farming? Even where primary forest is still intact, mammals are often scarce because of hunting pressures (Gola forest, Sierra Leone, personal observation; Korup National Park, Cameroon, J. Terborgh, personal communication). No amount of policing will stop people from hunting meat unless an alternative source of protein is found. Any plans for harvesting duikers would need to ensure careful control to safeguard against overexploitation. However, if such safeguards become possible, management of duikers in old farmland could take pressure away from rare species and from protected areas, while at the same time contributing to the wellbeing of the local people.

A necessary first step in this direction is the collection of basic information on the ecology and behaviour of free-living duikers in vegetation with different levels of disturbance. The southwest of Côte d'Ivoire provided a suitable study site because of the high density and relative ease of sightings of duikers within the National Park. In the present study, duiker populations were surveyed in forest near the research station of the Institut d'Ecologie Tropicale (IET) within the Park, and in secondary vegetation near the village of Gouleako. Information was collected opportunistically on diet, reproduction and other aspects of ecology. In addition, a more detailed study was carried out on the commonest species present, Cephalophus maxwelli.

1.2. Structure of the thesis

The remaining sections of this chapter give, firstly, a review of the literature on forest-living duikers, and secondly, a description of the study region. Chapter 2 describes the general methods used for the study, including the setting up of two study sites in forest and farmland. Chapter 3 describes the vegetation in each habitat in the two study sites, and Chapter 4 outlines phenological data in order to assess the availability of fruits as food for duikers.

The remainder of the thesis concentrates on duikers themselves. Chapter 5 summarises information collected on duiker diets, and relates it to phenological data; Chapters 6 and 7 give the results of the more detailed study of C. maxwelli. Chapter 6 outlines ranging patterns and habitat use, based mainly on the results of radio-tracking ten C. maxwelli over a period of 18 months. Chapter 7 presents data on various aspects of behaviour. Chapter 8 analyses population densities of duikers in the study sites and compares the efficacy of different population census methods.

Chapter 9 summarises the study; it also uses data on population densities and structure to outline population dynamics of C. maxwelli at Taï. Finally, implications for management and conservation are assessed.

1.3. Review of the literature on duikers of the genus Cephalophus

Duikers are antelopes of the subfamily Cephalophinae, within the family Bovidae. The Cephalophinae, which are found throughout sub-Saharan Africa, include two genera - Sylvicapra (one species) and Cephalophus (about 16 species - taxonomy is still unresolved). Duikers have been portrayed as frugivorous, nocturnal, monogamous animals which live in dense forest and hold small territories which are defended against conspecifics (eg. Dekeyser, 1956; Jarman, 1974; Ralls, 1970). In Jarman's classification of antelopes according to social organisation and ecology, duikers are lumped together with other small species such as Neotragus spp. (royal and Bates's pygmy antelopes - Feer, 1979), the suni (Nesotragus moschatus - Heinichen, 1972), and the dikdiks (Madoqua spp. - eg. Amubode and Boshe, 1990)), as being territorial and living alone or in pairs. Duikers are frequently likened to the ancestral ruminant which is thought to have been a small, solitary frugivorous forest-dweller (Geist, 1974).

The common duiker Sylvicapra grimmia and the red-flanked duiker Cephalophus rufilatus are savanna dwellers; many other species of Cephalophus are known to live in forest-savanna mosaics or in secondary thicket, as well as in primary forest. Since many forest species of Cephalophus live sympatrically (there are seven in Taï), there must be clear ecological divisions between them. One source of such divisions is undoubtedly body size - weights vary from 4 - 5 kg for the blue duiker (C. monticola) to 70 kg for the yellow-backed duiker (C. sylvicultor) and Jentink's duiker (C. jentinki). Variation in body size gives different options for diet (Hofmann, 1973), ranging, predator avoidance and habitat use. Other potential ecological dividers include activity patterns (diurnal, nocturnal or active both day and night), habitat specialisation, dietary specialisation and in conjunction with these, varying social systems.

Only three intensive studies of free-living forest duikers have been carried out to date. Dubost (1980) studied C. monticola in lowland rain forest near Makokou in Gabon; Feer (1988) studied C. dorsalis and C. callipygus at the same place; and Hart (1985) studied C. monticola and C. dorsalis in the Ituri forest in Zaïre. Apart from these, there are a number of records of anecdotal observations and captive studies. Table 1.1 gives body weights of the 16 species of Cephalophus and summarises information from the literature on activity patterns, habitat preferences and social systems. Dietary differences are dealt with briefly in the text below, and in more detail in Chapter 5.

Dubost and Feer carried out studies on artiodactyls at the same time that Gautier-Hion and others studied other frugivorous guilds such as primates and squirrels (Dubost, 1978, 1979, 1980, 1983, 1984, 1987; Dubost and Feer, 1988; Feer, 1979, 1988, 1989a, 1989b, in press; Gautier-Hion, 1990; Gautier-Hion et al, 1980, 1985a, 1985b), and this is the site at which niche separation between duikers is best understood. It contains six species of Cephalophus, all of which are primarily frugivorous. At least 68% of the mean dry weight of stomach contents for each species was made up of fruits and seeds, while 16 to 31% was made up of vegetative plant parts (Dubost, 1984). Two species have body weights which are very different from the rest - C. monticola, at only 5 kg, and C. sylvicultor, at 70 kg. Dubost (1984) showed that species of differing body weights eat different-sized food items - the larger the animal, the larger the food items - and this may be enough to define unique ecological niches for these two species. The remaining four species have body weights between 12 and 22 kg. C. nigrifrons is ecologically separate because it specialises in waterside habitats. C. dorsalis is the only nocturnal species within this size class, and Feer (1988) identified potential mechanisms by which its activity pattern could reduce niche overlap with diurnal species through a comparative study of C. dorsalis with the diurnal C. callipygus, which has a similar body weight. Both species are polygynous, and the females' ranges are of similar size. Both species are primarily solitary, especially C. dorsalis. However, C. callipygus is more highly frugivorous than C. dorsalis, eats a wider range of fruits and is more selective; it also travels further each day. Social organisation is distinct in that in C. callipygus, two females share a range, whereas C. dorsalis females have adjacent ranges. The differences in ranging and diet may be connected to a lesser abundance of fallen fruit at night; the difference in social structure may be because greater visual cues during the day-time allow C. callipygus more scope for a complex range of behaviour than the nocturnal C. dorsalis.

Only C. leucogaster and C. callipygus are not easily separated. They are within the same size class, both diurnal, and show no specialisations in habitat within the forest. However, their mean body weights are 13 kg and 20 kg respectively, which may be a large enough difference to reduce competition and niche overlap.

Present knowledge of West African duikers is less complete. All seven species found in forest in the Upper Guinean zone (west of the Dahomey Gap) are present at Taï. Apart from C. dorsalis (see above), none of them has been studied in the wild. C. jentinki is of the same size as C. sylvicultor but its ecology is almost unknown; its main habitat is dense forest (eg. Happold, 1973), but it has been reported to live near rivers or swamps (Kuhn, 1968) and come to the forest edge or even into farmland to feed on young shoots during the rainy season (Davies and Birkenhager, 1990). The Central African species C. monticola is replaced by C. maxwelli in West Africa, which although taxonomically very close to the former species is almost twice the size (see Table 1.1) and therefore not so clearly separated from the middle-sized species. C. maxwelli is thought to be active day and night (Aeschlimann, 1963; Ralls, 1973) or to be nocturnal (Baudenon, 1958); to prefer forest edge or secondary forest (Aeschlimann, 1963; Baudenon, 1958; Happold, 1973; Ralls, 1973), and probably to be territorial and polygynous (Aeschlimann, 1963; Happold, 1973; Ralls, 1973;

Ralls, 1975). The remaining species all have body weights between 12 kg and 25 kg - C. dorsalis (known to be nocturnal), C. zebra, C. ogilbyi and C. niger. Table 1.1 shows that knowledge of these last three species is minimal. C. zebra and C. niger are reported as living in "high forest"; for C. ogilbyi there are no reports even of habitat.

TABLE 1.1 - ECOLOGICAL FACTORS OF Cephalophus SPECIES

SPECIES	BODY WT (kg)[a]	ACTIVE (D/N/C)[b]	HABITAT PREFERENCES	SOCIAL SYSTEM
C. monticola	3-6	D[1,2,4] D+C[7]	Open parts of forest[1,4] Avoid big clearings and thick vegetation near villages[3,4] Forest, transitional woodland[25] Primary forest; prefer logged forest[25]	Monogamous pairs with young; territorial[1,4,5]
C. adersi	6-12	D[13]	-	
C. maxwelli *	9	D+N[8,12] N+C[11]	Prefer forest edge, around clearings[8,11] Prefer dense secondary thickets[12] Forest; sometimes secondary forest[26]	Probably territorial[8,10,12] Polygynous?[12] Territorial in captivity[26]
C. rufilatus	9-12	N+C[11] D[6] C[26]	Clearings[11] Gallery forest and forest edge[26]	Solitary[6,11] Polygynous?[6] Singles, pairs[26]

SPECIES	BODY WT (kg)[a]	ACTIVE (D/N/C)[b]	HABITAT PREFERENCES	SOCIAL SYSTEM
C. zebra*	9-15	-	Mature forest[22,26] often under red colobus or diana monkeys[22]	Singles[22]
C. natalensis	10-12	D[13]	Moist forest[25] Primary forest; prefer logged forest[28]	-
C. leucogaster	12-15	D[1,6]	Forest[26]	-
C. nigrifrons	13-16	D[1,6,15]	Riparian[3] High forest only, especially marshy areas[26]	Maybe territorial[15,6]
C. harveyi	13-16	D+N[13]	-	-
C. ogilbyi*	14-20	-	-	-
C. niger*	15-20	N[16,26]	Dense forest[11] High forest[26]	-
C. callipygus	15-24	D+C[1] D[6]	All forest types and edges; prefer dense undergrowth[1] High forest; sometimes secondary forest[26]	Males territorial[1] Polygynous[1] Solitary - one male has territory covering shared range of 2 females but animals move around independently[2]

[a] Body weights are taken from Wilson (1987), except for C. maxwelli which is taken from the present study.

[b] D = diurnal, N = nocturnal, C = crepuscular

* Species present in Taï

SPECIES	BODY WT (kg)[a]	ACTIVE (D/N/C)[b]	HABITAT PREFERENCES	SOCIAL SYSTEM
C. dorsalis*	19-25	N+C[1] N[2,14]	All forest types and edges; plantations at night[1] Dense forest[11] Forest[26]	Solitary; polygynous; probably territorial[1] One male has territory overlapping distinct ranges of 2 females
C. spadix	60	N[13]	-	-
C. jentinki*	70	-	Near water of swamps[21] Forest edge and farmlands in rainy season[26] Dense forest[26]	-
C. sylvicultor*	60-80	D+N[1,6] N+C[17,18] N[24,26]	"Thick bush"[17] Forest, bush, clearings, savanna[18] Forest edge and forest fragments[24] Mainly mature forest; also secondary forest[27]	Usually solitary[17] Maybe territorial pair with young[18] Groups of 1 - 4[13] In ones or twos, rarely small groups[24] Single/small groups[26]

References: [1] Feer (1988); [2] Hart (1985); [3] Dubost (1979); [4] Dubost (1980); [5] Dubost (1983); [6] Dubost and Feer (1988); [7] Crawford (1984); [8] Ralls (1973); [9] Ralls (1974); [10] Ralls (1975); [11] Baudenon (1958); [12] Aeschlimann (1963); [13] Kingdon (1982); [14] Henle and Apfelbach (1984); [15] Oboussier (1966); [16] Dittrich (1972); [17] Ansell (1950); [18] Lumpkin and Kranz (1984); [19] Rahm (1960); [20] Heinichen (1972); [21] Kuhn (1968); [22] Kuhn (1966); [23] Davies and Birkenhager (1990);[24] Dekeyser and Villiers (1955); [25] Ansell and Donsett (1988); [26] Happold (1973); [27] Wilkie (1987); [28] Nummelin (1990)

[a] Body weights are taken from Wilson (1987), except for C. maxwelli which is taken from the present study.
[b] D = diurnal, N = nocturnal, C = crepuscular
* Species present in Taï

1.4. Introduction to Taï

1.4.1. Description and history of Taï National Park Taï National Park lies between 5° and 7° N, in the rain forest belt of Côte d'Ivoire. It is to the west of the Sassandra river and about 15 km east of the Cavally river which forms the frontier with Liberia. Except for the extreme northernmost section, it is within the drainage area of the Cavally (Gartshore, 1989). The region contained a large "Refuge de flore et de faune" from 1926; the National Park was created in 1972, and a buffer zone was added in 1977 when it was declared a Man and the Biosphere Reserve. A map is given in Figure 1.1.

The Park consists of 340,000 ha of dense lowland rain forest interspersed with granite outcrops ("inselbergs"). A buffer zone covers an additional 96,000 ha, making it the largest protected area of forest in the Upper Guinean forest block. About 200,000 ha consists of untouched primary forest; much of the rest has been lightly logged in the 1960's and 1970's, including the study area at the research station of the Institut d'Ecologie Tropicale (IET - see Section 2.1). An aerial survey in 1988 confirmed that the interior of the Park remains in good condition, although the forest near the edges and in the buffer zone is seriously degraded in places.

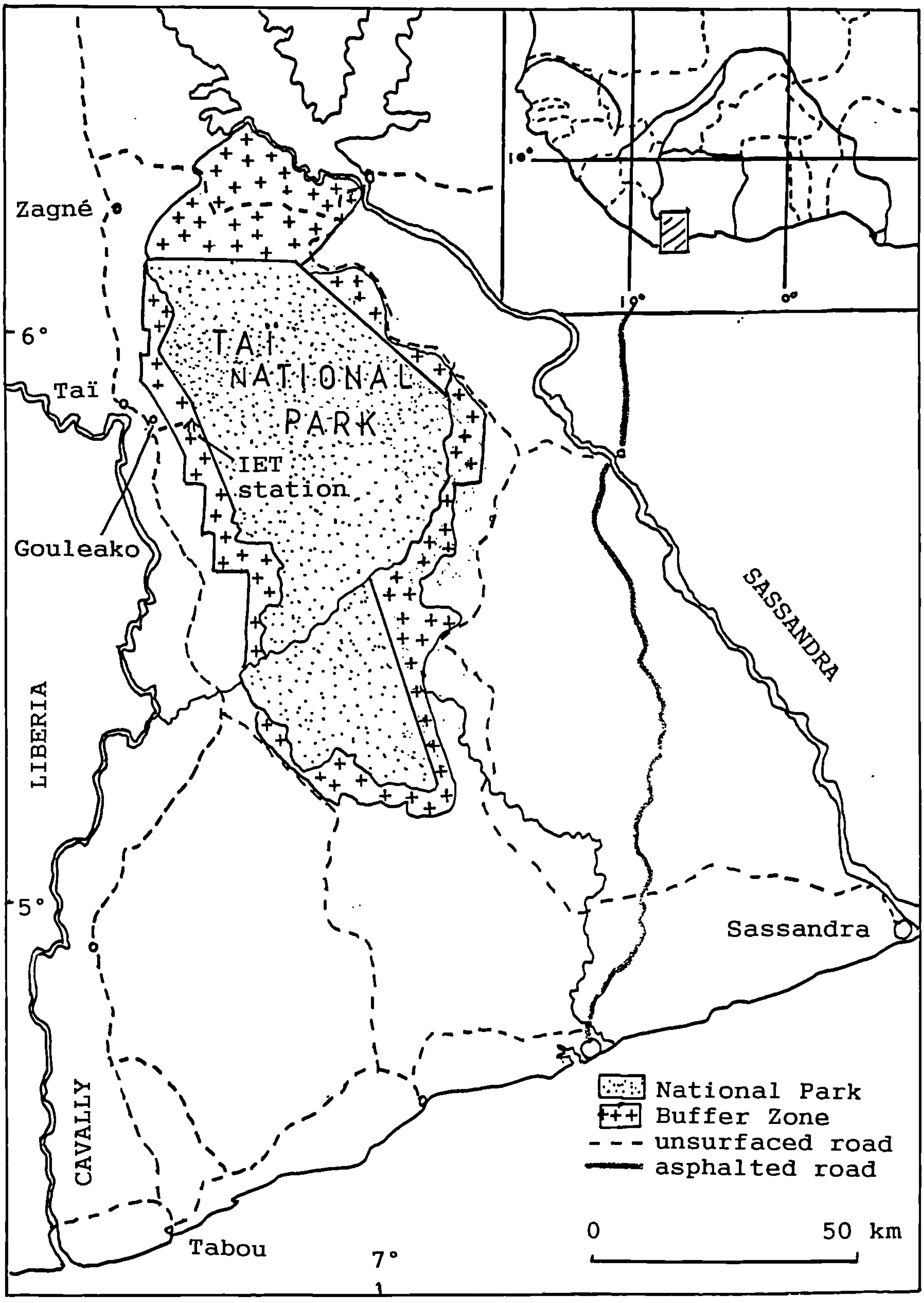
Poaching in most areas of the Park is frequent, and the population densities of some of the larger mammals have severely decreased. Forest elephants (Loxodonta africana *cyclotis*) were hunted almost to extinction in the late 1960's and 1970's, and it is estimated that only about 100 elephants survive (WWF, 1988). Forest buffalo (*Syncerus caffer nanus*) and bongo (*Boocercus euryceros*) are also reported by local people to be less common than previously, but are seen occasionally. However, all mammals typical of the Upper Guinean rain forest are still present, and mammal population densities at the study site around the IET station are still high, including species which are susceptible to hunting such as the red colobus (*Colobus badius*) and the leopard (*Panthera pardus*).

1.4.2. History and land use in the region around the Park

Until an access road was built from Guiglo to Djiroutou in the 1930's, the southwest of Côte d'Ivoire was very sparsely populated. Small, shifting communities of the Oubi, Guéré and Krou tribes practised hunting, fishing and cultivation for subsistence. Following construction of the road, permanent settlements were formed along its length, leaving the main forest area unpopulated.

Small-scale timber production was undertaken from this time, but no major changes took place until the 1960's, when the Government began a programme to develop the region. Logging became a major activity, and the Government encouraged the planting of cocoa and other tree crops. There was an influx of immigrants from areas where land was in short supply - firstly from the Baoulé region of central Côte d'Ivoire and then from the sub-Sahelian regions of Mali and Burkina Faso.

Figure 1.1 The location of Taï National Park (Côte d'Ivoire, West Africa)



The population density in the Taï "sous-préfecture" (the local administrative department) increased from 3.3 people per square kilometre in 1971 to 13 people per square kilometre in 1985, with immigrants outnumbering indigenous people by about four to one (de Rouw et al, 1990).

In 1988, a land use survey of the region between the Park and the Cavally river from the village Zaipobli to the village Para showed that no large tracts of primary forest remained outside the buffer zone to the Park, although there were forest fragments on cultivated land. Of the 79,240 ha surveyed, 23% was primary forest within the buffer zone; 50% was used for coffee or cocoa production by immigrants; a further 22% for mixed food and tree crops by both immigrants and indigenous people, and only 6% by indigenous people for rice, with some tree crops (de Rouw et al, 1990).

Land pressure in the area is now very great. The fallow period between rice plantings has been greatly reduced, and there are frequent disputes over land ownership as families find it harder to find land to farm every year. The problem was greatly exacerbated in 1990 and 1991 by the civil war in Liberia; over 400,000 Liberian refugees crossed the border into Côte d'Ivoire between Toulépleu in the north and Tabou on the coast. As a result, the population of the village of Taï increased ten-fold in the duration of this study.

There has been a corresponding increase in pressure on animal populations from hunting. Although all hunting is illegal in Côte d'Ivoire, bushmeat remains a major source of protein in rural areas and is also sold as a luxury item in top Abidjan restaurants (Adou, 1991). Hunting is carried out both in the mixed cultivated land near the villages and also in primary forest in the Park. Most villagers hunt mainly for private consumption by setting snares around their fields and in forest fragments, but each village has a small number of professional hunters who hunt with shotguns by night. The professional hunters prefer to hunt in the primary forest in the Park since visibility is very poor in dense secondary vegetation.

Around many villages such as Ponan to the north of Taï, almost all hunted species have nearly disappeared and the villagers recognise that soon there will be no animals to hunt. The land near Gouleako, where the second study site was situated, is adjacent to the Park and still had some fragments of degraded mature forest (See section 2.1 and Appendix 1(b)). Perhaps for these reasons, there are still populations of duikers and some monkey species. However, the situation with regard to both habitat destruction and hunting pressure is critical.

1.4.3. Climate The Taï region has a mean daily temperature of 25°C which varies little during the year, and mean annual rainfall which increases from 1700 mm in the north of the Park to 2200 mm in the south. The two study areas have a mean annual rainfall of 1900 mm. Relative humidity varies between 85% and 90% (GTZ, 1979).

There are two wet seasons each year, with peak rainfall typically in May to June and in September; however, rainfall patterns vary greatly from year to year. The long dry season lasts from December to mid-March, and is accentuated by the Harmattan wind, which brings cold, dusty air across from the Sahara, lowering both temperature and relative humidity. The short dry season is typically in August, but is extremely variable; it is often undetectable from rainfall patterns, but is characterised by increased solar radiation (Collinet et al, 1984).

Day-length varies from 11.75 hours in December (0625 to 1809 hours) to 12.5 hours in June (0607 to 1837 hours).

1.4.4. Flora As outlined in Section 1.4.1, the natural vegetation of Taï is dense lowland rain forest. The terrain consists of broad, often swampy river valleys alternating with gently sloping hillsides. A full vegetation description is given in Guillaumet (1967).

The region belongs to the Guinean forest block, which stretches from Guinea along the West African coast to the savanna gap in Ghana. There is an exceptional level of species endemism - of 868 higher plant species identified in the Park, 80% are endemic to the Guinean-Congo region, 16% to the Guinean region, and 8% (86 species) are endemic to the forest alongside the Cavally river which marks the Côte d'Ivoire - Liberia frontier. Guillaumet (1967) calls these species Sassandrian endemics, after the Sassandra river which is the first major biogeographical barrier to the east. The Taï National Park is the only protected area within this region of endemism.

Plant species composition changes through the Park from north to south with increasing rainfall, and also with local variations in soils and moisture conditions. A number of authors have developed classification systems to identify the different forest types and these are summarised in Chapter 3 (based on de Rouw et al, 1990, chapter 7).

Much of the Park underwent selective logging in the 1960's and 1970's. However, the original structure and floristic composition has largely been retained; only the larger trees of important timber species were cut (GTZ, 1979). These include Afzelia bella var. gracilior ("doussié"), Khaya ivorensis ("acajou blanc"), Lovoa trichilioides ("dibetou"), Tarrieta utilis ("niangon"), Terminalia ivorensis ("framiré") and Turraenthus africanus ("avodiré").

Secondary growth occurs on sites of shifting cultivation during the fallow period, and also in plantations of coffee and cocoa. The species richness and composition and the structure of secondary forest vary greatly according to the history of disturbance. De Rouw et al (1990) sampled forest fallows aged 5 to 12 years and identified two distinct secondary forest communities at the latitudes of the present study. Type I was present over the entire toposequence except the valley bottoms and was characterised by woody lianas such as Rutidea parviflora (Rubiaceae), Secamone afzelii (Asclepiadaceae) and the genera Dioscorea (Dioscoreaceae) and Clerodendrum (Verbenaceae). Type II secondary forest occurred mainly in valley bottoms and, occasionally, lower slopes; characteristic species were lianas and pioneer trees such as Cleistopholis patens (Annonaceae) and Ricinodendron heudelotii (Passifloraceae).

The GTZ report (1979, pp. 21 - 22) describes secondary growth of different ages, dividing it into secondary thickets, which are rich in herbaceous plants such as Aframomum spp. (Zingiberaceae) and in young shrubs and trees in an early phase of growth (Musanga spp., Moraceae; Anthocleista nobilis, Loganiaceae); young secondary forests, which have a dense understorey and few herbaceous plants; and old secondary forests, which have a structure similar to that of primary forest although with a greater density of small trees.

In old or poorly managed coffee and cocoa plantations, a thicket develops which is composed mainly of grasses and the invasive forb Chromolaena odorata (ex Eupatorium odoratum, Compositae). (de Rouw et al, 1990). Well-managed plantations are cleared of undergrowth every three or four months, and only woody species resistant to repeated cutting survive.

Undergrowth in plantations is characterised by the lianas *Clerodendrum* spp. (Verbenaceae) and *Morinda longiflora* (Rubiaceae).

1.4.5. Fauna Vertebrate fauna recorded in the Taï forest are discussed below, with the emphasis on species which are likely to affect duikers, either as competitors or as predators.

1.4.5.1. Mammals Appendix 2 lists 154 mammalian species recorded for the Taï region. Fruit-eating mammals, which may either be in competition with duikers for food or may facilitate duiker foraging by dislodging fruit from the trees, include guenon monkeys (*Cercopithecus spp*.), collared mangabey *Cercocebus torquatus* and chimpanzee *Pan troglodytes* among the primates; water chevrotain (*Hyemoschus aquaticus*) and bushpig *Potamochoerus porcus* among the ungulates; squirrels (Sciuridae), flying squirrels (Anomaluridae) and fruit-bats (Megachiroptera). The main mammalian predators on duikers are the leopard (*Panthera pardus*) and man; the golden cat *Felis aurata* may also take infant duikers. Folivorous ungulates such as the royal antelope *Neotragus pygmaeus* and the bushbuck *Tragelaphus scriptus* may compete with duikers of comparable body size for resting-places.

Few data are available on the presence of mammalian species in areas of secondary growth in the Park. Roth and Merz (1986) conducted a census of tracks and pellets along two tracks through secondary growth areas and found more signs of buffalo and leopard in secondary growth than in primary forest, but less of duikers; however, they suggested that this may have been due to variation in the favourability of substrate conditions in preserving tracks and dung in the different sites. Therefore the present summary concentrates on primary forest communities.

1.4.5.2. Other vertebrates Birds have been extensively studied in the area and 207 species have been identified (Gartshore, 1989), including the rare white-breasted guinea-fowl (*Agelastes meleagrides*) and four other Red Data Book species. Large frugivorous birds include hornbills, three species of turaco and three species of parrot. The only raptor likely to take duiker is the crowned hawk-eagle (*Stephanoaetus coronatus*).

Herpetofauna include the three species of crocodile found in Côte d'Ivoire (*Crocodilus cataphractus*, *C. niloticus* and *Osteolaemus tetraspis*) (Guillaumet and Boesch, 1984), and at least 33 species of snake (Cordellier, 1984) of which the most frequently seen poisonous ones include green mamba (*Dendroaspis viridis*), forest cobra (*Naja melanoleucus*), green tree viper (*Atheris clorechis*) and Gaboon viper (*Bitis gabonica*). The python, which is known to prey on duiker elsewhere (eg. Henle and Apfelbach, 1985) is present in the Park but is not common - none were seen during the present study.

CHAPTER 2. GENERAL METHODS

In this chapter, general methods are described for setting up study sites, recording rainfall, habitat classification, capture of duikers, radio-tracking, direct observation of duikers, and mapping of latrine distributions. More specific methods are described in the following chapters as necessary.

2.1. Set-up of Study Sites

Two study sites were chosen which contrasted markedly in vegetation. One site was in primary lowland forest which had been lightly logged in the 1970's; it was situated near the research station of the Institut d'Ecologie Tropicale (IET) in Taï National Park. The second site was about 10 km to the west, just outside the Park, on the land of the village of Gouleako. As is typical in the region, small-scale farming had created a patchwork of degraded forest, secondary thickets, bamboo, fields of rice and other crops, and coffee and cocoa plantations. The two sites will be referred to throughout as IET and Gouleako; maps are given in Appendix 1. Each site was about 1 km^2 in area.

In order to facilitate capture and tracking of duikers, a grid system of trails was created in each site, with grid-cells of about 100 m x 100 m. Maintenance of trails was kept to a minimum to avoid unnecessary disturbance, but in secondary vegetation at Gouleako the trails quickly became overgrown, and had to be re-cleared before each visit.

2.2. Rainfall

Daily readings of rainfall (March 1990 - November 1991) were made in the early mornings from a rain gauge located in a small clearing about 500 m from the IET research station. Monthly totals are presented in Appendix 3. These data were used in analysis of phenological patterns, reported in Chapter 4.

2.3. Habitat Classification

2.3.1. IET At the IET site, only two forest types were distinguished, as follows:

Bas-fond (BF) - Valley bottoms with deep, permanently damp soils rich in organic matter. Vegetation of these areas has been characterised by either palm trees (*Raphia* spp., Palmaceae) and lianescent palms (*Calamus* spp. and *Eremospatha* spp. (Palmaceae)) or mixed dicotyledonous trees such as *Anthocleista vogelii* (Loganiaceae), *Carapa procera* (Meliaceae), *Dialium dinklagei* (Caesalpinaceae), *Gilbertiodendron* spp. (Caesalpinaceae), and *Xylopia parviflora* (Annonaceae). Characteristic herbaceous plants include *Sarcophrynium brachystachyium* (Marantaceae) *Marantochloa purpurea* (Marantaceae), *Costus* spp. (Zingiberaceae) and *Aframomum* spp. (Zingiberaceae). (GTZ report, 1979; Kahn, 1984).

High forest (FH) - This term will be used to include all mature forest above the level of the Bas-Fonds, on valley sides and on summits.

2.3.2. Gouleako At Gouleako, mature forest was classified as above, but differed from IET in that all forest patches had been cut continuously for wood for use in the village. There was a noticeable lack of large trees, a less complete canopy than at IET, and denser shrub layer.

Areas of secondary vegetation were defined by present land use (if any) and the age of the secondary growth, which was determined by interviews of the villagers. Villagers were questioned on the age of each patch of secondary growth at least twice and consistency was found to be very high. Secondary growth was divided into thickets, with no canopy layer, and young secondary forest, where a broken canopy had begun to form. In addition to cultivated areas and secondary growth there were stands of bamboo on the site. Besides the two categories for mature forest, six habitat categories were used:-

JF2 - young secondary thicket (less than 7 years' growth). Corresponds approximately to "fourrés secondaires" in the GTZ report (1979, p.21).

JBF - young Bas-Fond (thicket)

VF2 - young secondary forest with a broken canopy (more than seven years' growth). Corresponds approximately to "jeunes forêts secondaires" in the GTZ report.

EUP - thickets of Chromolaena odorata (Compositae), an introduced species which commonly covers abandoned fields in the first year after cultivation

CHA - land under cultivation - fields of rice, maize and other food crops; plantations of coffee and cocoa

BAM - stands of bamboo (Bambusa vulgaris, Gramineae)

2.4. Capture of Duikers

It was necessary to catch duikers primarily in order to attach radio-collars. In the second year of the study, additional captures were made in order to collect blood and rectal faecal samples and to gather data on populations. It took three months to develop an effective capture method; a complete account of the methods tried is given in Appendix 4. The methods which proved most suitable for this study are described below.

During the study, 41 captures were made - 39 C. maxwelli and two C. dorsalis. Details of captured animals are given in Appendix 5.

2.4.1. Methods

2.4.1.1. Day-time net-capture One-hectare blocks were enclosed by eight 55 m nets, following a standard method for catching small forest ungulates (eg. Bourquin and Bourquin, 1984; Feer, 1988; Harding, 1986). The nets used were each 55 m long by 1.5 m high and were made of black nylon with a 2.5 cm diamond mesh. A minimum of 12 people were needed, and worked in four teams, one on each side of the block. The nets were attached with nylon cords at the top to trees and were pegged to the ground every one or two metres with wooden pegs. Logs were used to block holes around obstructions such as fallen trees.

It took about 45 minutes to erect the nets. In mature forest, people then searched through the block and chased any duikers they found into the nets. However, this was not possible in the thick undergrowth at Gouleako, so once the nets were in place, extra transects were cut across the hectare to divide it in four, and each quarter was searched separately. Four people worked their way through the quarter in a line, using machetes where necessary to clear a passage, making much noise and paying special attention to treefalls and thickets where duikers often lie hidden. If a duiker was seen it usually ran into another quarter of the block and the nets were moved to enclose it in a smaller area. Eventually it would be enclosed in one of the quarter blocks and chased into a net. Each block took three or four hours to sample by this method. When an animal was caught, it was put in a sack and hung from a tree, where it would stay quietly until we had finished the chase. All animals were released at the place of capture within 20 minutes from the time of capture.

This method was labour-intensive, time-consuming, and minimally productive because few duikers were encountered. After initial trials it was used at the IET site only when we were re-catching radio-collared animals or their mates, and could locate the animals before putting up the nets. However, in Gouleako the method continued to be used since the encounter rate was higher and no effective alternative was found.

2.4.1.2. Night-time net-capture method Seven people walked transects at night between 2100 hours and 0500 hours. Two people walked 20 to 30 m ahead of the group and searched for duikers with head-torches. Duiker eyes reflect yellow or orange in torchlight. When a duiker was found, it was dazzled with a very strong torch (Mag-lite 5 D-cell) and it usually froze. The rest of the team then approached and while one person kept the torch on the duiker's eyes, the other six worked in pairs to encircle it at a distance of 5 to 15 m with three nets. Once the nets were up, the duiker was flushed into them.

2.4.2. Data recorded

The following data were recorded for each duiker caught:

Sex, age class and reproductive status (i.e. if lactating or pregnant)
Body weight (kg)
Number of erupted cheek-teeth
Place, time and date of capture
Alone or with other duikers when caught

Age class was determined for duikers caught by the number of erupted maxillary molars and by body size, and from duikers observed by body size and behaviour, as follows. Young, unweaned animals which spent most of the time lying hidden were classified as infants. These were under 3 months old (see chapter 7). After an initial capture of one infant individual under 4 kg in weight, infants were not caught, in order to minimise disturbance. At about three months, they began to move around and forage for food; they were then about two thirds the height of the adults (see chapter 7) and were referred to as juveniles. Comparison with growth curves of *C. dorsalis* and *C. callipygus* (Feer, 1988) and the common duiker *Sylvicapra grimmia* (Wilson *et al*, 1984) suggests that this category is likely to have included animals up to an age of about 10 months. This was also the age of eruption of the second molar. One Maxwell's duiker caught during the present study which was known to be approximately ten months old had a half-erupted second molar, and Feer (1988) and Wilson *et al* (1984) found that for *C. dorsalis*, *C. callipygus* and *S. grimmia*, the first molar erupted within the first three months of life, and the second molar at about nine or ten months. Among captured animals, those with a single molar were classified juveniles, and those with a second molar fully erupted were classified as M2, whilst those with the third molar also fully erupted were classified as adults. The adult category will have included subadults which were not yet sexually mature. During observations in the forest, the classes of M2 and adult were not distinguished.

Sheep-tattooing equipment was used to tattoo a number in one ear of all adults and subadults caught, for identification on recapture. All adults and subadults caught up to January

1991 were fitted with a Telonics radio-collar (Section 2.5.1). All animals caught in 1991 were sampled for blood and faeces for hormonal analysis at London zoo and parasitic analysis at the University of Wageningen, Holland. From November 1991 they were also marked with sheep sprays to aid recognition in the field for capture-recapture studies (see Chapter 8).

2.5. Radio-tracking

At IET, six Maxwells' duikers were radio-collared between May and October 1990 - three adult males, two adult females and a juvenile female. At Gouleako, four Maxwells' duikers were radio-collared between August 1990 and January 1991 - two adult males, an adult female and a juvenile female.

2.5.1. Equipment Ten radio-collars with MOD-315 transmitters set between 148 and 150 MHz were supplied by Telonics for use on the duikers. Each collar had a different frequency, allowing them to be distinguished during remote tracking. The transmitters were equipped with S9 mercury tilt-switches which cause a change in transmission rate from 50 to 75 pulses per minute when the head is moved down, thus allowing remote monitoring of active and resting phases. The collars could be adjusted for neck circumferences of 16 to 30 cm, and had 40 cm antennae which were partly encased in the collar material. A TR-2 Receiver with a 3-element Yagi antenna was used for tracking.

2.5.2. Tests of Accuracy of Bearings Before radio-collars were attached to duikers, a number of trials were carried out to test the performance of the radio-tracking equipment in the two study sites. The trials tested the accuracy of bearings taken at different distances from the target transmitters; this, in turn, determined the accuracy with which duikers could be tracked when out of sight and was thus a key factor in the planning of the radio-tracking study.

2.5.2.1. IET

Nine collars were set out at known locations along a 200 m transect, and bearings were taken from positions at 25 m intervals along a baseline at right angles to the transect. Bearings were taken by two methods - firstly, from the direction of the strongest signal, and secondly from the direction midway between the points of signal fall-off. The second method was the more time-consuming, but because of the receiving characteristics of the 3-element Yagi antenna, it has been reported to be more accurate (eg. Kenward, 1987). It was found that the direction of the strongest signal was often impossible to locate directly, since the signal could be almost equally strong over a broad span of directions; therefore, the bisection of the points of signal fall-off was used.

Of 28 bearings, three could not be defined because of strong, diffuse back signals. Apart from these, the angular error (that is, the difference between the observed and actual compass bearings) varied between 1° and 62° ($x = 16°$, $n = 25$). There was no correlation between angular error and transmitter-receiver distance (Spearman's ρ = 0.07, n.s.). These angular errors are very large, probably because of the dense undergrowth and high humidity (cf. Hupp and Ratti, 1983). It was concluded that triangulation from fixed stations was not possible.

Additional tests were carried out at IET to see how accurately a collar could be located by repeated triangulation as the collar was approached. This was done within the known limits of the home range of the first duiker to be radio-collared (Mae Mae). The range was almost all in the BF region of a single valley, and was therefore almost entirely flat. Nine collars were placed at random coordinates within the limits of the range by an assistant. Bearings were then taken from two or more different points and the position of the collar was calculated by triangulation, using a Hewlett-Packard 32S pocket calculator programmed for this purpose. When a position had been calculated, the author approached that place, occasionally checking the radio signal to see if the bearing changed, and if necessary took bearings for further triangulation to home in on the collar. Each time a bearing was taken, the author's position and the bearing obtained were noted. Once the collar's true position was known, the angular error of each bearing was calculated.

For a total of 28 bearings, the range of angular errors was 0° to 45°, with a mean of 15°. There was no correlation between angular error and transmitter-receiver distance (Spearman's ρ = -0.32, n.s.). Moreover, although the received signal usually became stronger as the author approached the transmitter, this relationship was not reliable since the signal sometimes stayed constant or became fainter. Therefore, signal strength alone was not a reliable indicator of the distance to a collar. However, with practice a collar hidden in the forest could quickly be located.

2.5.2.2. Gouleako At Gouleako, tests could be done only on the transects, because of the dense vegetation. The author stood at the intersection of two transects, and an assistant in radio contact with the author moved around the far sides of each adjacent 100 m x 100 m grid-cell, stopping every 25 m while the author took a bearing. Thus, the tests covered a range of distances from 100 m to 142 m. This was done in two different locations. Angular errors ranged from 0° to 56° (mean = 15°); of 34 bearings, 21 would have given an error in location of greater than 25 m at the far side of a grid-cell, and 12 would have given an error of greater than 50 m. In an attempt to improve bearing accuracy, the tests were repeated with the receiving antenna raised on a 3 m pole. However, there was only a slight improvement:- after 17 bearings angular error ranged from 1° to 43° (mean = 12°); ten bearings would have given an error of location greater than 25 m, and three an error greater than 50 m.

2.5.3. Conclusions Angular errors were found of up to 62° at IET and 56° at Gouleako, apart from frequent back-signals. It was concluded from these tests that the use of triangulation in tracking duikers at either of the study sites was not justified. Instead, radio-tracking was used for direct observation of duikers in order to study behaviour (see section 2.6 below), and also to locate animals to the nearest grid-cell to study ranging patterns and the use of space (see Chapter 6).

2.6. Direct observations of duikers

The best way to gather information on the behaviour and ecology of duikers would be to observe them directly. However, they are shy and silent and visibility in the forest rarely exceeds 20 m. Some forest animals, in particular primates, have been successfully habituated to the presence of human observers so that almost continuous observation is possible (eg. Fossey, 1983), but although attempts were made to habituate collared individuals, it was never possible to follow them by sight. Therefore, radio-tracking was used to locate each animal and maximise the number of encounters with a minimum of disturbance, which gave a series of short observations as the animal passed by. The best method of making observations involved two observers in contact by hand-radios; one monitored the radio-signals and attempted to predict where the duiker would go, and the other hid in order to observe it passing by. This worked moderately well for all individuals except one - the juvenile female (Gabrielle) was so timid that she was seen only ten times during one and a half years of radio-tracking, and was hard to catch at the end of the study because she would flee at the first approach of the capture team, even at night.

Direct observations were also made in a number of other ways. Observers hid at duiker latrine areas within the ranges of radio-collared animals and made notes on all duikers which visited. At the end of the study some simple hides were made from palm leaves. Some very close observations of duikers were made from the hides, but they still tended to be very brief since the duikers spent most of the time on the move.

Data were also gathered from all opportunistic sightings of both collared and non-collared animals throughout the study.

The following information was recorded as far as possible for each observation:-

Time and location
Reaction of animal to observer
Duration of observation
Direction of travel
Feeding
Activity
Group size and composition
Group leadership and spacing during travel
Social interactions

Observer-animal distance

The methods of analysis of these results are given in Chapter 5 for feeding; Chapter 7 for activity, group size, group composition, group leadership, spacing during travel, and social interactions; and Chapter 8 for observer - animal distances.

2.7. Territorial marking: Latrine distribution

It quickly became apparent that C. maxwelli habitually use certain areas for defaecation, thus forming latrines. By mapping the latrines, three benefits were foreseen:- firstly, to find good places for observation of duikers; secondly, to determine the social significance of latrines (see Chapter 7), and thirdly, to determine the effect latrine distribution was likely to have on population density estimates based on transect censuses of dung (see Chapter 8). An intensive search for latrines was possible only at IET, since at Gouleako the vegetation was too dense.

To determine the distribution of latrines, the four home-ranges determined at IET by radio-tracking were searched intensively by a team of three to five people for pellet groups.

First, the people formed a line, each about 3 metres from their neighbour, and walked in parallel across the area being searched at a rate of about 10 metres per minute. Each person scanned a strip of ground to the front and sides while walking along, so that all the area between searchers was covered. The searchers kept in a line at a constant distance apart to ensure that no areas were missed. Each searcher carried a stick, which was used to move vegetation aside in thick areas such as treefalls and allow a clear view of the forest floor. The searcher at one end of the line put up fluorescent marker ribbons at intervals, so that when the search-line was finished, the adjacent strip could be searched following the markers. A short rest was taken after each 400 to 600 metres to regain concentration. In this way an area of 30 hectares was covered.

When a pellet group was found, it was marked with a fluorescent ribbon (low down, to avoid confusion with direction markers), and the approximate location was noted so it could be found again. In the second stage of the search, a more intensive search was made at each place where pellets had been found. The searchers advanced in a line shoulder to shoulder, using small sticks to move vegetation and debris. An arbitrary distance of 6 metres was chosen as the maximum at which adjacent pellet groups were counted as in the same latrine; the limits of the latrine were defined by a 6-metre outer margin which an intensive search proved free of pellets.

CHAPTER 3. VEGETATION

3.1. Introduction

The purpose of this chapter is to look at aspects of vegetation which are especially important to duikers. These include the presence and abundance of plant species which serve as food and the structure of the vegetation up to a height of one metre above the ground, which determines both visibility and ease of passage for duikers. Phenology will be dealt with in Chapter 4, and implications for duiker habitat use and preferences will be discussed in chapters 5, 6 and 9.

The two study sites were divided into vegetation types at the start of the study according to age of vegetation and the position on valley bottoms (BF) or slopes and crests (FH). These vegetation types were clearly distinctive in the field, and are described in section 2.3.1. Plants were surveyed in each vegetation type.

The following summary of previous vegetation classification systems used in Taï is adapted from de Rouw et al (1990, Chapter 7).

Mangenot (1955, in de Rouw et al, 1990) and Guillaumet (1967) classified undisturbed mature forest according to a number of species groups. In Mangenot's system, groups M1, M2 and M3 should be present throughout the Taï region, M4 should occur in sandy soils, M5 to M7 in increasingly moist conditions, M8 in valley bottoms, and M9 in valley bottoms which are mudflats. Guillaumet's group G1 occurs on all except poorly drained primary forest; G2 on sandy soils; G3 on finer-textured soils, G4 in addition to G3 and G1 on areas where water availability and growth conditions are very good. G5 species occur in valley bottoms, accompanied by G6 in clayey areas. G7 species occur on organic soils, and G8 on alluvial deposits.

De Rouw et al's system (1990) includes both undisturbed forest and 5 to 12 year secondary vegetation. Sixteen communities are defined by the presence or predominance of each of 29 sociological species groups (SSG's). The area of the present study falls within de Rouw's Land Unit type Unm2, characterised by upland forest type A (SSGs 1, 2, 3, 8 and 29) and secondary forest types I (SSGs 23 and 24) and II (SSGs 23 and 25). De Rouw et al (1990) includes full lists of the species assigned to each species group in the three above systems.

3.2. Plant Species Surveys

3.2.1. Methods Trees and ground plants were surveyed separately in each vegetation type except fields (CHA), which were omitted because of a lack of trees and a preponderance of fast-changing cultivars on the ground.

Data on trees were gathered primarily to allow comparison with previous studies of vegetation types in Taï, but are also complementary to phenology data, giving information on the fruit likely to be found in each vegetation type (See Chapters 4 and 5). Ground plants were defined, for the purposes of this study, as plants with leaves lower than 1.2 m from the ground - the estimated maximum browsing height for the largest duikers. Data on ground plants thus gave information on leaves available to duikers, as well as fruits which are produced near the ground. Data were gathered in June 1991 during the short rainy season, when a minimum of plants would be missed due to dormancy.

Five blocks of each vegetation type were selected at each site. In each block, species of small plants were recorded in six 2m x 1m quadrats randomly placed by the side of a transect, with an estimated percent cover for each species in each quadrat (<10%. 10-25%, 25-50%, 50-99%, 100%). The quadrat was then extended to a 2m x 2m square and on each side, the nearest tree greater than 5 cm diameter at breast height was identified, then its distance from the quadrat and its circumference were measured. Thus, a sample of 120 trees was obtained for each vegetation type.

For all habitats at Gouleako, additional notes were made in each block on structure and estimated height of vegetation, visibility at eye-level and noticeably predominant plant species.

The data for trees and ground plants were analyzed separately. In each case, two multivariate analysis techniques were used to look at the variation between blocks and between vegetation types - an ordination by detrended correspondence analysis (DCA) and a classification by two-way indicator species analysis (for theoretical background see Gauch 1982). The analyses were carried out on a VAX computer using the programs CANOCO and TWINSPAN respectively. In addition, the most abundant families and species were identified both for the whole data set and for each vegetation type.

It should be emphasised that the analyses by CANOCO and TWINSPAN are not hypothesis-testing statistical analyses; rather, they provide ways of presenting clear patterns from complex data sets. A detrended correspondence analysis (DCA) uses a modified reciprocal averaging technique to represent samples in two- or multi-dimensional space such that similar samples are close together and dissimilar samples are far apart. Axes are identified during the analysis which will emphasise variation across the community; the axes can often be related post-hoc to environmental gradients. Two-way indicator species analysis (TWINSPAN) divides a data set into two clusters such that the variance within each cluster is less than the variance between the clusters. This is done successively for each sub-group, producing a hierarchical classification of samples or species which can be represented as a dendrogram. TWINSPAN is thus complementary to DCA in that it emphasises differences between samples rather than trends across samples in the community. The program also lists "indicator species" for each cluster at each level of division.

3.2.2. Results

All plant species recorded are listed in Appendix 6.

3.2.2.1. Trees Samples of trees were incomplete in two vegetation types (Bamboo, n=96 and Chromolaena, n=105) because occasionally no tree was present between one or more sides of the quadrat and the edge of the vegetation block. Therefore the total number of trees recorded was 1041, representing 46 families, 130 genera and 171 species. Only two trees remained unidentified.

Figure 3.1 shows the results of the DCA ordination of the tree data at the level of blocks of each vegetation type. Bamboo samples were omitted after an initial analysis since they were extremely distinct from all other vegetation types, and determined the first axis. The analysis gave four axes but only the first two are shown since their eigenvalues are high[1] (axis 1, 0.73; axis 2, 0.58) and the third and fourth axis showed no further separation of vegetation types. The figure confirms the classification used for the four mature vegetation types; the samples for each vegetation type are located in a distinct cluster. The secondary vegetation types are less distinct, with no clear separation of young secondary dry forest (JF2) and young bas-fond (JBF). Chromolaena and old secondary vegetation (VF2) each show three blocks which are grouped apart

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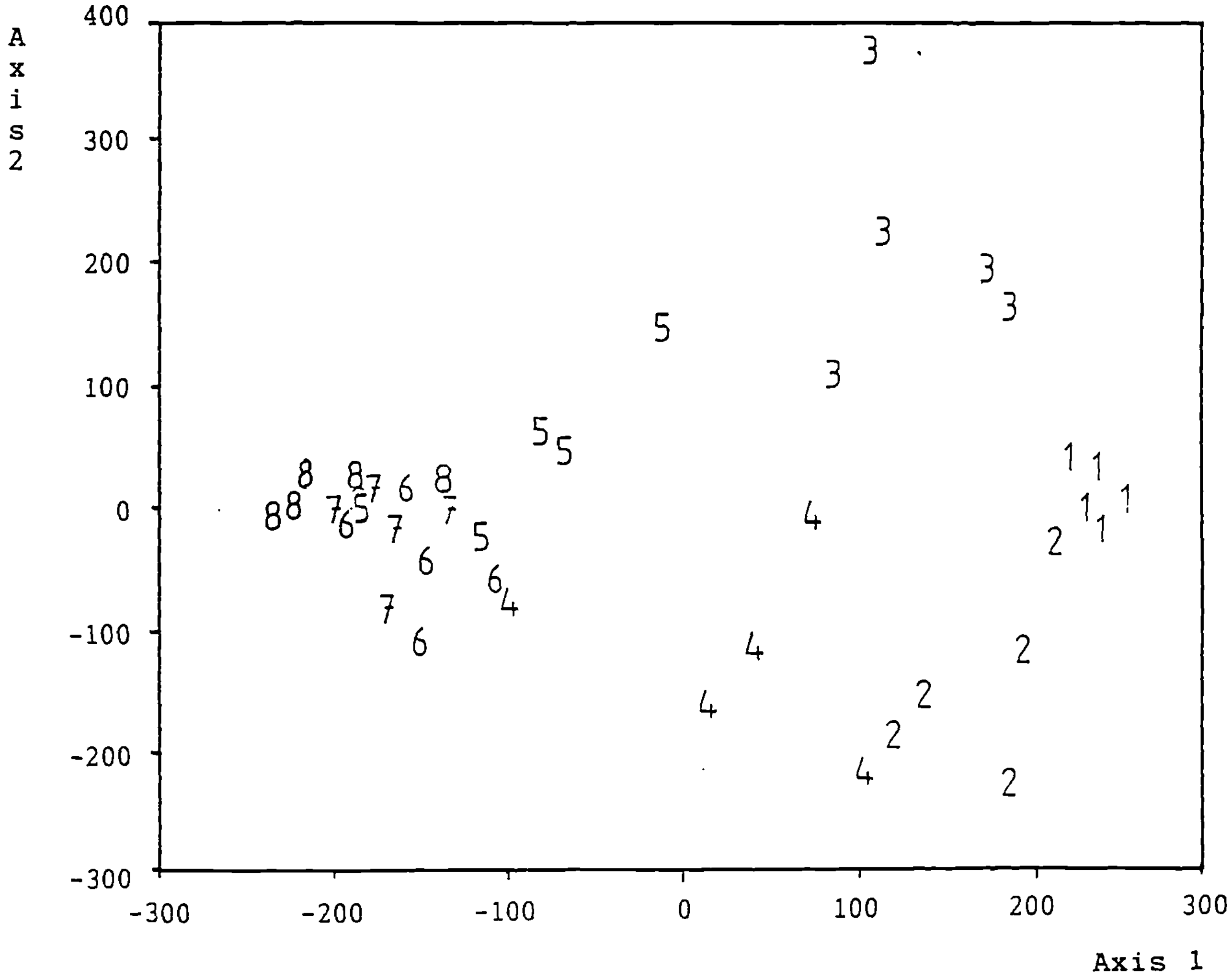
[1] The eigenvalue indicates the proportion of the total remaining variance accounted for by the axis.

from all other samples, and two blocks overlapping with the locations of JF2 and JBF.

It can be seen that axis 1 represents a gradient of habitat disturbance, with more disturbed habitats to the left and less disturbed habitats to the right. Axis two shows a gradient from wet to dry habitats, with bas-fond habitats at the bottom and drier habitats towards the top.

Figure 3.2 shows the results of the TWINSPAN analysis of tree data for each block of each vegetation type. The first division separates primary forest habitats and bamboo from secondary habitats; indicator species for primary forest were Diospyros mannii (Ebenaceae) and Strombosia glaucescens (Olacaeae), and for secondary vegetation were Macaranga barteri, M. hurifolia, Rauvolfia vomitoria (Euphorbiaceae), Zanthoxylon macrophyllum (Rutaceae) and Ficus capensis (Moraceae). As in the ordination analysis, further division of secondary vegetation types is not clear-cut. However, the five blocks of young secondary forest (JF2) are all very similar, staying together in the analysis even after the sixth level of division. The sixth level indicator species for the cluster is the coloniser species Musanga cecropioides (Cecropiaceae).

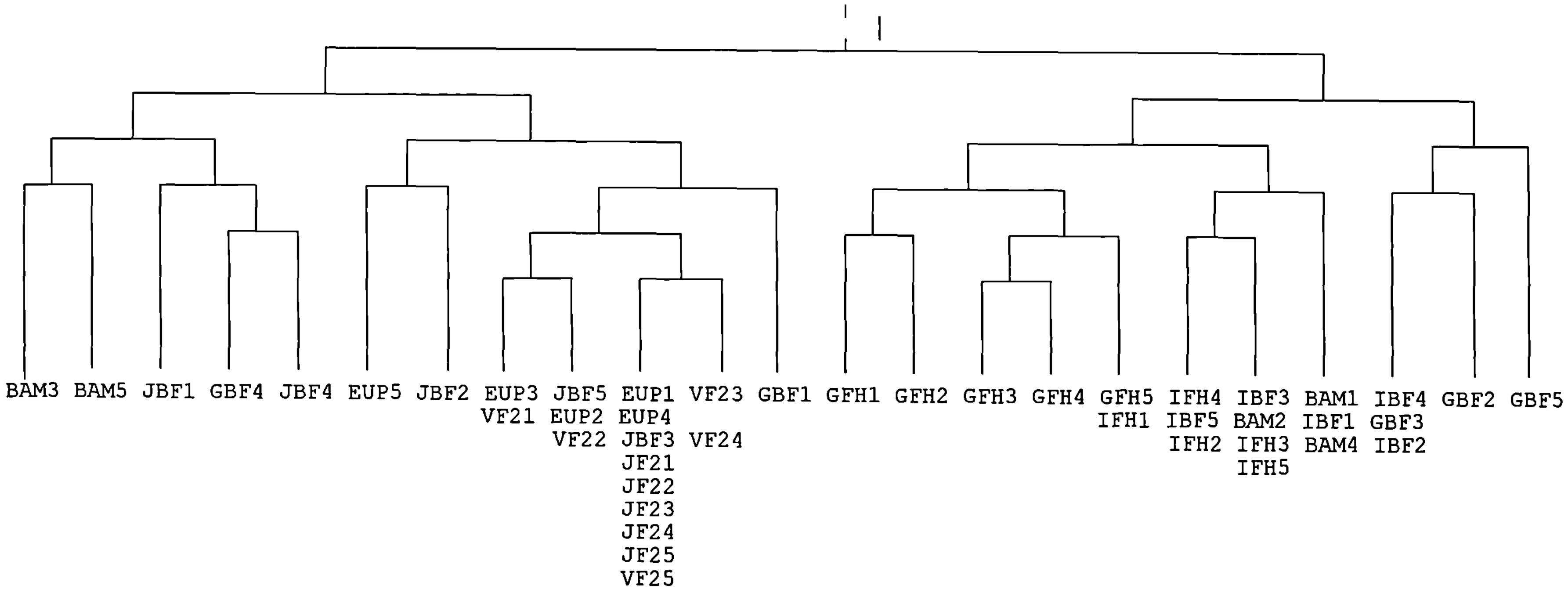
Figure 3.1
DCA Analysis of tree data (excluding bamboo), by blocks



Key to habitats

1 = IFH (IET mature forest); 2 = IBF (IET Bas-Fond); 3 = GFH (Gouleako mature forest); 4 = GBF (Gouleako Bas-fond); 5 = VF2 (Old secondary forest); 6 = JF2 (young secondary forest); 7 = JBF (young Bas-fond); 8 = EUP (Chromolaena thicket). See Section 2.3 for descriptions of habitats.

Figure 3.2 TWINSPAN analysis of tree data, by blocks



KEY

BAM = Bamboo; GFH = Gouleako mature forest; JF2 = Young secondary forest;
EUP = Chromolaena thicket; IFH = IET mature forest; VF2 = Old secondary forest;
GBF = Gouleako Bas-Fond; JBF = Young Bas-Fond; IBF = IET Bas-Fond

The second level division of primary forest types separates five blocks of bas-fond, characterised by the species *Raphia sassandriensis* (Palmaceae), from the remaining bas-fond and all mature dry forest blocks. *R. sassandriensis* forms areas of palm swamp which were very distinctive in the field. The third-level division separates all mature dry forest at Gouleako and one block at IET from the rest at IET plus three blocks in bamboo. Gouleako mature dry forest (GFH) is characterised by *Rinorea longicuspis* (Violaceae).

Tables 3.1 and 3.2 show the five most common families and species respectively over the whole data set, and for each vegetation type. 226 of the 1041 trees recorded belonged to the family Euphorbiaceae, which was the most common family in all secondary vegetation types and was in the top four for all other types. About half of these trees (117) were *Macaranga* spp., which is a genus of secondary colonisers. *M. barteri* was the most common species in old secondary forest, and *M. hurifolia* in young bas-fond and *Chromolaena* thickets. *Rauvolfia vomitoria* (Euphorbiaceae) was the commonest species in young secondary forest. Palmaceae was the most common family in the IET swamp forest and the second most common in the Gouleako primary and secondary swamp forest. Only three species were recorded: *Raphia sassandriensis*, the most common species in mature bas-fond (both at IET and Gouleako); *R. hookeri*, a climbing

Table 3.1 Most abundant five families of trees for each vegetation type and overall

Vegetation types	Rank				
	1	2	3	4	5
IFH	Ebenaceae	Annonaceae	Rubiaceae	Euphorbiaceae	Olacaceae
IBF	Palmaceae	Rubiaceae	Euphorbiaceae	Ebenaceae	Sterculiaceae
GFH	Violaceae	Euphorbiaceae	Caesalpiniaceae	Annonaceae	Ebenaceae
GBF	Euphorbiaceae	Palmaceae	Sterculiaceae	Meliaceae	Caesalpiniaceae
VF2	Euphorbiaceae	Apocynaceae	Flacourtaceae	Annonaceae	Caesalpiniaceae
JF2	Euphorbiaceae	Apocynaceae	Guttiferae	Cecropiaceae	Mimosaceae
JBF	Euphorbiaceae	Palmaceae	Rubiaceae	Guttiferae	Cecropiaceae
EUP	Euphorbiaceae	Apocynaceae	Mimosaceae	Cecropiaceae	Moraceae
BAM	Gramineae	Euphorbiaceae	Anacardiaceae	Annonaceae	Meliaceae
ALL	Euphorbiaceae	Palmaceae	Ebenaceae	Apocynaceae	Annonaceae

KEY TO VEGETATION TYPES BAM = Bamboo; IFH = IET climax forest; EUP = *Chromolaena* thicket; JBF = Young Bas-Fond; GBF = Gouleako Bas-Fond; JF2 = Young secondary forest; GFH = Gouleako climax forest; VF2 = Old secondary forest; IBF = IET Bas-Fond

Table 3.2 Most abundant five species of trees for each vegetation type

Vegetation types	Rank				
	1	2	3	4	5
IFH	*Diospyros mannii*	*Diospyros soubreana*	*Craterispermum caudatum*	*Xylopia quintasii*	*Strombosia glaucescens*
IBF	*Raphia sassandriensis*	*Tarrietia utilis*	*Gaertnera paniculata*	*Scytopetalum tieghemii*	*Diospyros mannii*
GFH	*Rinorea longicuspis*	*Microdesmis puberula*	*Cleistanthus polystachyus*	*Strombosia glaucescens*	*Polyalthia oliveri*
GBF	*Raphia sassandriensis*	*Macaranga hurifolia*	*Raphia hookeri*	*Tarrietia utilis*	*Carapa procera*
VF2	*Macaranga barteri*	*Macaranga hurifolia*	*Mareya micrantha*	*Caloncoba brevipes*	*Rauvolfia vomitoria*
JF2	*Rauvolfia vomitoria*	*Macaranga barteri*	*Macaranga hurifolia*	*Harungana madagascariensis*	*Bridelia grandis*
JBF	*Macaranga hurifolia*	*Raphia hookeri*	*Tetrorchidium didymostemon*	*Harungana madagascariensis*	*Musanga cecropioides*
EUP	*Macaranga hurifolia*	*Rauvolfia vomitoria*	*Ficus capensis*	*Funtumia elastica*	*Musanga cecropioides*
BAM	*Bambusa vulgaris*	*Spondianthus preussii*	*Lannea welwitschii*	*Anthocleista vogelii*	*Trichilia heudelottii*

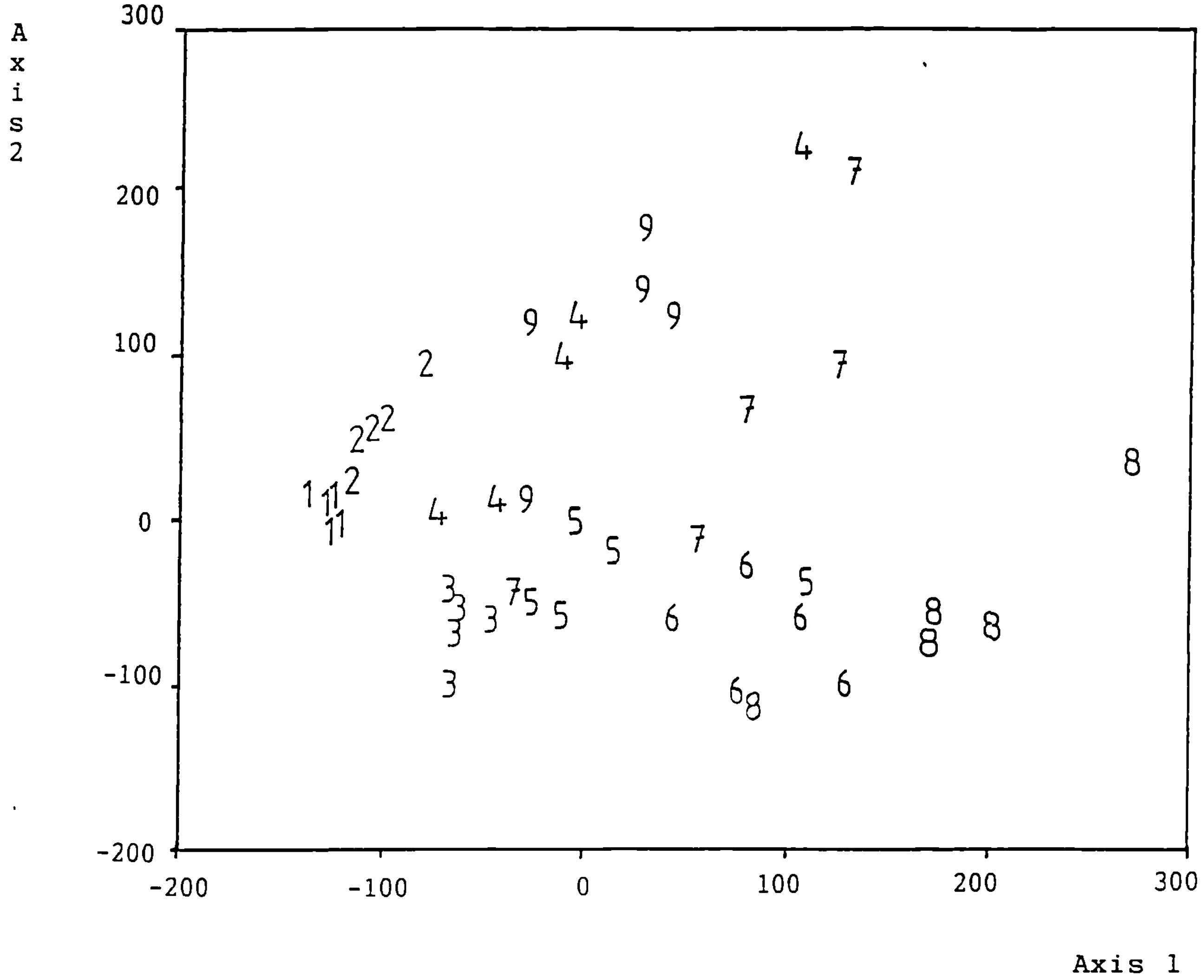
KEY TO VEGETATION TYPES BAM = Bamboo; IFH = IET climax forest; EUP = *Chromolaena* thicket; JBF = Young Bas-Fond; GBF = Gouleako Bas-Fond; JF2 = Young secondary forest; GFH = Gouleako climax forest; VF2 = Old secondary forest; IBF = IET Bas-Fond palm found in disturbed swamp vegetation (both mature and young bas-fond at Gouleako); and Elaeis guineensis (the oil palm), found in dry secondary vegetation. Ebenaceae was the most common family in the IET mature dry forest; five species were recorded, all from the genus Diospyros. D. mannii and D. soubreana were the commonest two species in IET mature dry forest. These trees are commonly cut for building materials, which explains their lower abundance at Gouleako. Bamboo patches were dominated by Bambusa vulgaris (Gramineae), although they were by no means monostands - only 44 of 96 'trees' recorded were bamboo. In the Gouleako mature forest the commonest family was Violaceae, due to the abundance of Rinorea longicuspis (recorded 23 times in a data set of 120).

3.2.2.2. Ground plants The total number of records of plants was 2946, representing 79 families, 280 genera and 432 species. Since all species present in each of the thirty samples in each vegetation type were recorded, the number of records for a species within a vegetation type varies from 0 to 30.

Figure 3.3 shows the results of the DCA ordination of the ground plant data, at the level of blocks of each vegetation type. As with the tree data, only two axes are used (Eigenvalues 0.51, 0.38) because further axes did not further clarify the separation of vegetation types. The four mature vegetation types are again clearly separated in two-dimensional space, although ground plants are similar in Gouleako bas-fond and in bamboo. The four secondary vegetation types (*Chromolaena*, young bas-fond, young and old secondary forest) each have four samples which are distinct from all other vegetation types and one sample which overlaps with other secondary vegetation. The first axis reflects a gradient from old, undisturbed vegetation to young, disturbed vegetation; the second axis shows a gradient from dry to wet habitats.

Figure 3.4 shows the results of the TWINSPAN analysis of ground-plant data for the blocks of each vegetation type. The first division splits off three bas-fond blocks and one bamboo block, with indicator species *Palisota barteri* (Commelinaceae) and *Halopegia azurea* (Marantaceae). The rest of the samples are then divided into young secondary forest (JF2) and four of the five *Chromolaena* blocks in one group, characterised by *Chromolaena odorata* (Compositae); and mature habitats, bamboo and all but one block of old secondary forest in another group, characterised by *Diospyros mannii*, *D. soubreana* (Ebenaceae), *Dialium aubrevillei* (Caesalpiniaceae) and *Neuropeltis acuminata* (Convolvulaceae). The third-level division of the latter group separates all IET bas-fond and three of five IET mature dry forest blocks from the remainder; the indicator species are the forest tree species

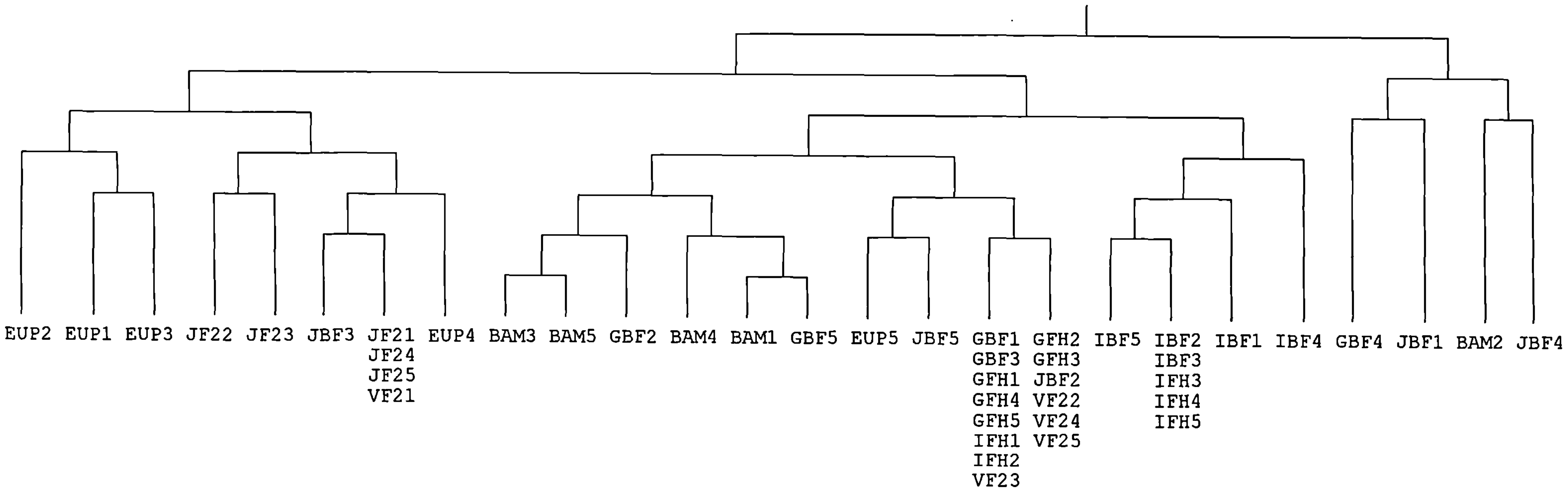
Figure 3.3
DCA Analysis of small plant data, by blocks



Key to habitats

1 = IFH (IET mature forest); 2 = IBF (IET Bas-Fond); 3 = GFH (Gouleako mature forest); 4 = GBF (Gouleako Bas-fond); 5 = VF2 (Old secondary forest); 6 = JF2 (young secondary forest); 7 = JBF (young Bas-fond); 8 = EUP (Chromolaena thicket). See Section 2.3 for descriptions of habitats.

Figure 3.4. TWINSPAN analysis of small plant survey, by blocks



KEY

BAM = Bamboo; GFH = Gouleako mature forest; JF2 = Young secondary forest;
EUP = *Chromolaena* thicket; IFH = IET mature forest; VF2 = Old secondary forest;
GBF = Gouleako Bas-Fond; JBF = Young Bas-Fond; IBF = IET Bas-Fond

Diospyros mannii (Ebenaceae), Xylopia quintasii (Annonaceae) and Aphanostylis leptantha (Apocynaceae), and the ground plants Geophila afzelii and G. hirsuta (Rubiaceae). Blocks of young bas-fond vegetation are not clustered together.

Tables 3.3 and 3.4 show the five most common families and species respectively over the whole data set, and for each vegetation type. The most commonly occurring family overall was the Rubiaceae (333 of 2946 species records), representing 44 species, which was also the commonest family in all secondary vegetation types except Chromolaena thickets, and in IET bas-fond. 144 of these records were of the genus Geophila, small ground-covering plants. Geophila afzelii was the most common species in the IET bas-fond and in young secondary forest (JF2) and within the top five species for all vegetation types except Gouleako mature dry forest and Gouleako bas-fond. The most common family in the Chromolaena vegetation type was Compositae; the defining species, Chromolaena odorata, was recorded in 29 of the 30 samples. The second most common family overall, and the commonest in IET mature dry forest, was the Ebenaceae; six species of Diospyros were recorded. Diospyros mannii was the most common species in IET mature dry forest, occurring in 26 of 30 samples. The commonest family in Gouleako mature dry forest and in Gouleako bas-fond was Araceae, represented by Culcasia

Table 3.3 Most abundant five families of ground plants for each vegetation type

Vegetation types	Rank				
	1	2	3	4	5
IFH	Ebenaceae	Rubiaceae	Annonaceae	Apocynaceae	Caesalpiniaceae
IBF	Rubiaceae	Ebenaceae	Annonaceae	Apocynaceae	Marantaceae
GFH	Araceae	Rubiaceae	Convolvulaceae	Connaraceae	Violaceae
GBF	Araceae	Marantaceae	Rubiaceae	Euphorbiaceae	Caesalpiniaceae
VF2	Rubiaceae	Euphorbiaceae	Araceae	Convolvulaceae	Gramineae
JF2	Rubiaceae	Euphorbiaceae	Compositae	Mimosaceae	Violaceae
JBF	Rubiaceae	Euphorbiaceae	Commelinaceae	Compositae	Araceae
EUP	Compositae	Rubiaceae	Gramineae	Caesalpiniaceae	Euphorbiaceae
BAM	Rubiaceae	Araceae	Apocynaceae	Euphorbiaceae	Piperaceae
ALL	Rubiaceae	Ebenaceae	Euphorbiaceae	Araceae	Apocynaceae

KEY TO VEGETATION TYPES BAM = Bamboo; IFH = IET climax forest; EUP = Chromolaena thicket; JBF = Young Bas-Fond; GBF = Gouleako Bas-Fond; JF2 = Young secondary forest; GFH = Gouleako climax forest; VF2 = Old secondary forest; IBF = IET Bas-Fond

Table 3.4 Most abundant five species of ground plants for each vegetation type

Vegetation types	Rank				
	1	2	3	4	5
IFH	Diospyros mannii	Dialium aubrevillei	Geophila afzelii	Strombosia glaucescens	Xylopia quintasii
IBF	Geophila afzelii	Aphanostylis leptantha	Diospyros mannii	Geophila hirsuta	Xylopia quintasii
GFH	Neuropeltis acuminata	Rinorea longiscuspis	Culcasia mannii	Strombosia glaucescens	Tiliacora dinklagei
GBF	Halopegia azurea	Culcasia parviflora	Cercestis afzelii	Pteris burtonii	Afrosersalisia afzelii
VF2	Neuropeltis acuminata	Geophila afzelii	Scleria barteri	Cercestis afzelii	Ctenitis vogelii
JF2	Geophila afzelii	Chromolaena odorata	Tetracera potatoria	Rinorea longicuspis	Scleria barteri
JBF	Chromolaena odorata	Geophila afzelii	Sabicea discolor	Cyclosorus oppositifolius	Cercestis afzelii
EUP	Chromolaena odorata	Tetracera potatoria	Geophila afzelii	Griffonia simplicifolia	Scleria barteri
BAM	Cercestis afzelii	Piper guineense	Landolphia owariensis	Neuropeltis acuminata	Geophila afzelii

KEY TO VEGETATION TYPES BAM = Bamboo; IFH = IET climax forest; EUP = Chromolaena thicket;
JBF = Young Bas-Fond; GBF = Gouleako Bas-Fond; JF2 = Young secondary forest;
GFH = Gouleako climax forest; VF2 = Old secondary forest; IBF = IET Bas-Fond

spp. and Cercestis afzelii. However, the commonest species in these two vegetation types were Neuropeltis acuminata (Convolvulaceae) and Halopegia azurea (Marantaceae) respectively.

3.2.3. Discussion Summarising the results of the TWINSPAN and ordination analyses, the main division in species composition for both trees and ground plants is between older forest types and young secondary vegetation. For trees, mature forest types (IBF, IFH, GBF and GFH) and bamboo are separate from all secondary vegetation types; for ground plants, old secondary forest (VF2) is included in this group. The analyses of both tree and ground plant data support the distinction made between bamboo stands and forest, and the division of mature forest into FH and BF at each site. All bamboo stands were situated in valley bottoms, and ground plants in bamboo stands proved similar to those in GBF. The results of TWINSPAN highlight an additional division to be made between palm swamps dominated by Raphia sassandriensis (Palmaceae) and other areas of BF.

Secondary habitat divisions are less clearly upheld by the analyses. The ordinations show that VF2, JF2 and EUP formed a gradient based on the age of vegetation, but there was an overlap between classes for both trees and ground plants. JF2 and JBF overlapped almost completely in the ordination of tree data, but were distinct in ground plants. In the field, JBF areas were distinguished from other areas of secondary vegetation both by waterlogged soil and by the presence of ground plants typical of bas-fond (Marantaceae). JF2 and EUP are grouped together in the TWINSPAN analysis for ground plants. These two habitats became increasingly hard to separate during the year as Chromolaena monostands, growing on fields abandoned shortly before the start of the study, became invaded by shrubby vegetation.

If we compare the present results with the classification systems outlined in Section 3.1, we find a general correspondence, although some of the species mentioned as important in previous studies were unrecorded in the present study, and vice versa. Mangenot and Guillaumet's systems were restricted to mature growth, so only the BF - FH division is relevant. Taking the five most common tree species recorded in each of IBF, GBF, JBF and bamboo, only five of a total of twenty are included in Mangenot's system - two M7 species, one M8 species, and two M3 species. Twelve of the twenty top trees in the above vegetation types are included in Guillaumet's system, of which two are G1, one G3, two G4, three G5 and four G7. Thus, the species which overlap between this study and previous ones suggest that the present BF category corresponds adequately to Mangenot and Guillaumet's valley bottom areas, with a predominance of M7 and M8 or G5 to G7 species.

In de Rouw's system, type A climax forest is characterised by sociological species group 1 (SSG1), named by species Hunteria simii (Apocynaceae) and Chidlowia sanguinea

(Caesalpiniaceae). However, in the present study there were no records of Hunteria simii and only one record of Chidlowia sanguinea. Of seventeen other species in SSG1, six were unrecorded and five were recorded only once. None were key species for TWINSPAN divisions. The reason for this major discrepancy is unknown, but is likely to be due to patchiness in species composition within de Rouw's land unit Unm2. The most common species found in mature upland forest (GFH and IFH) were all SSG29, which de Rouw found throughout upland forest types. The most common species in BF and bamboo were mostly of SSG's 4, 5 and 6. Group 4 and 5 were recorded by de Rouw in valley bottoms within Unm2, and Group 6 specifically in swamps.

Turning to upland secondary vegetation (VF2, JF2, EUP), the most common species recorded in this study belong to SSG's 4, 5, 23 and 29. Group 23 was found by de Rouw to be common to all secondary forest from 5 to 12 years old; it is clear from the present study that it is also present in younger secondary vegetation.

In conclusion, data on species composition confirm the division of primary forest into upland forest (FH) and Bas-Fond (BF); they also point to a distinction between the two study sites for each of these vegetation types. There is a continuum in species composition of young secondary growth from Chromolaena thickets to young and older secondary forest. Bamboo stands show a ground flora close to that of

Gouleako Bas-Fond. Young Bas-Fond was not clearly defined by the analyses, but shows similarities both to upland vegetation of a similar age (JF2, VF2) and to mature Bas-Fond.

3.3. Vegetation Structure

Vegetation structure affects duikers in two ways. Firstly, it determines the ease of passage of a duiker through the undergrowth; secondly, it determines visibility, which is important in searching for food, in maintaining contact with conspecifics, and in vigilance for or concealment from predators. Five of the seven duiker species at Taï have a shoulder height between 30 cm and 50 cm; one of the largest of these, C. niger, can stretch its head up to a height of 83 cm to pick vegetation (personal observation). Vegetation structure was measured up to a height of 85 cm to maximise its relevance for these smaller, more common species of duikers.

3.3.1. Methods Vegetation structure was measured primarily by an index of visibility. A 50 cm x 85 cm piece of black polythene was painted with a checkerboard of white and black 5 cm x 5 cm squares and attached to two poles along the sides. The poles extended 20 cm beyond the edge of the polythene at one end. The poles were held upright on the ground with the polythene pulled flat between them, making a vertical checkerboard raised 20 cm from the ground. The experimenter squatted on the ground 10 m away, with her eyes at a height of approximately 40 cm (comparable to a Maxwell's duiker). She then counted the number of white squares which were at least partly visible through the foliage without moving her head. If the position of the board fell in a hollow so that the change in level of the ground obscured the board, the bases of the poles were held at the height of the surrounding ground so that the squares could be counted through the vegetation as normal. Two measures of visibility were taken at six places in five blocks of each vegetation type at each study site, in May 1991.

The results were analyzed for differences between vegetation types using a one-way ANOVA and two-tailed t-tests.

3.3.2. Results A one-way ANOVA on visibility in the nine different vegetation types was highly significant ($p<0.001$).

Table 3.5 - Vegetation types in order of decreasing mean visibility; results of t-tests.

	IBF	IFH	BAM	GFH	GBF	VF2	JF2	JBF
IFH	ns	-						
BAM	**	*	-					
GFH		*	ns	-				
GBF			*	ns	-			
VF2				**	ns	-		
JF2					**	ns	-	
JBF						***	ns	-
EUP							***	***

* $p<0.05$ ** $p<0.01$ *** $p<0.001$

Table 3.5 shows the vegetation types in order of decreasing mean visibility; without exception, visibility was greatest in the oldest vegetation types and decreased as the vegetation became younger. T-tests were applied to adjacent columns in the table, and where these were not significantly different, to the next nearest column until a significant difference was found. The results are shown in the table.

3.3.3. Discussion The results show no significant differences in visibility between FH and BF in mature forest, but they do confirm that younger vegetation types have lower visibility than older ones.

Impressions in the field add to the picture. At IET it was possible to walk easily in the forest, apart from thickets (see below); at Gouleako it was noticeably harder to walk through the mature forest or old secondary growth, and impossible to walk through young secondary growth without damaging the vegetation. This finding will be linked to duiker habitat preferences in Chapter 6.

In mature forest, thick patches of undergrowth of two types are encountered - thickets of climbing palms (Eremospatha hookeri and Calamus deerratus) in bas-fond areas, and thickets at tree-falls ("chablis") in all forest types. It is very likely that duikers use such areas for cover, but since duikers could not be located accurately enough to quantify their use of small thickets, these areas were not studied separately.

CHAPTER 4. PHENOLOGY

4.1. Introduction

Duikers are thought to be primarily frugivorous (eg. Feer, 1988; Hart, 1985, Ralls, 1970; see also Sections 1.3 and 5.1), so food distribution and abundance of food depend on the fruiting patterns of food species. Thus it is important to understand fruiting cycles and their causes.

Rainfall is an important proximate factor in the determination of fruiting cycles, but such cycles are also evolutionarily advantageous because of biotic factors such as pollinators and seed predators or dispersers. Most biotic factors affect the degree of clumping of flowering and fruiting rather than the actual time of year (van Schaik et al, 1993). For example, Augspurger (1982) showed that for one species of shrub on Barro Colorado Island in Panama, flowering was induced by the first moderate rain after a drought in the dry season. If a single shrub was induced to flower at a different time, it failed to attract insect pollinators down from the forest canopy, and seeds were heavily predated by caterpillars, but if a group of shrubs were all induced to flower together out of season, they attracted pollinators and caterpillar predation was reduced. In Borneo, masting reduces the effects of seed predation by producing a short-term superabundance of seeds so that predators are satiated and destroy only a small percentage of the seeds (Terborgh, 1990). Gautier-Hion (1990) tested the relative importance of biotic and abiotic factors in determining fruiting patterns in Gabonese rain forest by comparing species which suffered major seed predation after dispersal with animal-dispersed species which did not suffer major seed predation. According to the predator satiation hypothesis, the former should synchronise fruiting, while the latter should space fruiting out so as to reduce competition for animal dispersers, but this was not the case. Species with different dispersal mechanisms (zoochorous or animal-dispersed, anemochorous or wind-dispersed, and autochorous or self-dispersed) had very similar fruiting patterns. However, different growth forms of plants and different types of fruit did show different fruiting patterns, suggesting that abiotic factors were most important. Most dehiscent fruits (including both animal-dispersed and non-animal-dispersed species) matured in the dry season, while most fleshy fruits matured in the wet season.

Alexandre (1980) studied monthly fruit production during the course of a year near the IET station at Taï and looked in more detail at the relation between dispersal mechanisms, growth forms and fruit sizes for trees over 20 m high. He found the following relationships:-

Autochores - produced September to January, peaking in November (end of the rainy season). Mostly from trees 20 - 30 m high.

Anemochores - produced mostly October to April, peaking in March (end of the dry season). Mostly from trees over 35 m high.

Zoochores - produced throughout the year but with a peak in December (middle of dry season). Mostly from trees 25 - 35 m high.

Zoochores were by far the largest class, forming 76% of all tree species over 20 m high that were recorded, and the overall pattern of fruiting was largely determined by that of zoochorous species, with a peak in December.

The number of species in fruit each month was positively correlated with the rainfall of three months previously, with a peak in the middle of the main dry season, in December. The quantity of fruit produced showed no such pattern, and peaked slightly later in January.

Van Schaik et al (1993) reviewed the literature on biotic and abiotic factors affecting phenological events. They found that water-stress is the primary factor inducing leaf-flush and flowering; however, where there is no water-stress, these events coincide with the season of maximum insolation. Thus, community peaks in leaf-flush and flowering (but not fruiting) follow the path of the zenithal sun across the intertropical convergence zone.

Since little information was available at the start of the study on the dietary importance of different plant species, a general phenological study was undertaken to outline seasonality of production and availability of fruit in the two sites and in different habitats. Two methods were used to monitor fruit production - collection from fruit traps, which reflected fruit production at the time of the collection, and collection from the ground, which showed what was available for duikers to eat at any one time, after consumption by other animals and including fruits and seeds which last on the forest floor long after production has stopped. Both types of collection are commonly used in studies of this kind and a comparison was made at IET by using both methods in parallel. Fruit traps were not used in Gouleako since the site was on land used regularly by villagers.

4.2. Methods

Fruit quadrats At each site, 51 1m x 2m quadrats were marked out with canes once a month from December 1990 to November 1991 at random locations along the transect system. Quadrats were placed alternately on the left and right sides of the transects. For each quadrat, the location and habitat was noted, and all fruits, flowers and seeds within the quadrat were collected. Fruits and seeds which were thoroughly decayed were discounted; immature fruits were counted, but noted as immature.

Fruit traps 51 1m x 1m traps were made of plastic sacking and suspended with nylon cords at a height of about 1.2m. A small square was cut from the centre of each trap and the hole was covered with fine-mesh mosquito netting, which acted as an outlet for rainwater. One trap was placed randomly in each 100 m stretch along five parallel transects at IET, each between 500 m and 1400 m long. During a trial period from June to October 1990, sacks were emptied once a week, but many of them collected no fruit in a week, so subsequently they were emptied once every two weeks for a full year from December 1990 to November 1991.

For both traps and quadrats, the number of fruits, flowers and loose seeds of each species was recorded from each sample, and then samples were combined for the whole collection on that date, dried in a simple solar drier, and the total dry weight for each plant part and species was recorded. Reference specimens of each species were stored in 30% ethanol and drawings and descriptions were made of each species for later identification.

In the analysis of results, the predominant species of fruits, seeds and flowers were identified. Trap data were then analyzed to look at overall seasonal patterns of fruit, flower and seed production and to test for correlations between production and rainfall. As far as possible, fruit species were classified as zoochorous, anemochorous or autochorous so that seasonal patterns of these three groups could be compared. Production was also compared in the two habitats distinguished at IET.

Quadrat data were used to determine fruit, flower and seed availability on the ground and to compare the two sites. Comparisons were made using Friedman and Wilcoxon tests.

Data collection was aimed primarily at a comparison between the two sites through randomly placed quadrats. For this reason, quadrat numbers were not balanced between habitats. Therefore, in order to compare habitats, the average weight per quadrat of fruits, flowers and seeds in each habitat was calculated for each collection and the results were compared using the Wilcoxon test. Young Bas-Fond (JBF) was excluded from these analyses due to small sample sizes.

Seasonal patterns and distributions between habitats of individual species will be discussed in more detail after presentation of material on duiker diets (See Chapter 5).

4.3. Results

The ten species and plant parts making up the greatest weight over the year are listed below for each type of collection.

At IET in both traps and ground quadrats, predominant species included Sacoglottis gabonensis, Parinari excelsa, Pentadesma butyracea, Dialium aubrevillei and Diospyros sanzaminika. In traps, Chrysophyllum taiense fruits and seeds and Scottelia chevalieri flowers were also predominant; in ground quadrats, Klainedoxa gabonensis and Copaifera salikounda were more prevalent. These differences may be methodological; on the ground, large items may be over-represented compared to small items because the latter decay more quickly or are missed in the leaf litter. Alternatively, species which are less common on the ground than in fruit traps may be those which are preferentially eaten by ground frugivores. Only one species predominant in ground quadrats at Gouleako was different from those at IET - Ricinodendron heudelottii, which is a species listed by de Rouw *et al* (1990) as characteristic of secondary growth on agricultural land.

IET TRAPS:
1 *Chrysophyllum taiense* fruit (Sapotaceae)
2 *Sacoglottis gabonensis* fruit (Humiriaceae)
3 *Pentadesma butyracea* fruit (Guttiferae)
4 *Dialium aubrevillei* fruit (Caesalpiniaceae)
5 *Scottelia chevalieri* flower (Flacourtiaceae)
6 *Diospyros sanzaminika* seed (Ebenaceae)
7 *Chrysophyllum taiense* seed (Sapotaceae)
8 *Diospyros sanzaminika* fruit (Ebenaceae)
9 *Parinari excelsa* fruit (Chrysobalanaceae)
10 *Dialium aubrevillei* seed (Caesalpiniaceae)

IET QUADS:
1 *Parinari excelsa* fruit (Chrysobalanaceae)
2 *Sacoglottis gabonensis* fruit (Humiriaceae)
3 *Parinari excelsa* seed (Chrysobalanaceae)
4 *Pentadesma butyracea* fruit (Guttiferae)
5 *Diospyros sanzaminika* fruit (Ebenaceae)
6 *Klainedoxa gabonensis* fruit (Simaroubaraceae)
7 *Diospyros sanzaminika* seed (Ebenaceae)
8 *Dialium aubrevillei* fruit (Caesalpiniaceae)
9 *Sacoglottis gabonensis* seed (Humiriaceae)
10 *Copaifera salikounda* fruit (Caesalpiniaceae)

GOULEAKO QUADS:
1 *Ricinodendron heudelottii* fruit (Euphorbiaceae)
2 *Pentadesma butyracea* flower (Guttiferae)
3 *Dialium aubrevillei* fruit (Caesalpiniaceae)
4 *Parinari excelsa* seed (Chrysobalanaceae)
5 *Pentadesma butyracea* fruit (Guttiferae)
6 *Sacoglottis gabonensis* fruit (Humiriaceae)
7 *Diospyros sanzaminika* fruit (Ebenaceae)
8 *Parinari excelsa* fruit (Chrysobalanaceae)
9 *Diospyros sanzaminika* seed (Ebenaceae)
10 *Dialium aubrevillei* seed (Caesalpiniaceae)

Total dry weights of fruits, flowers and seeds recorded in each collection from fruit traps are represented in Figure 4.1.

Looking at overall seasonality from fruit traps, there was a rise in flower production from December to the end of February. Fruit production was also greatest from December to the beginning of

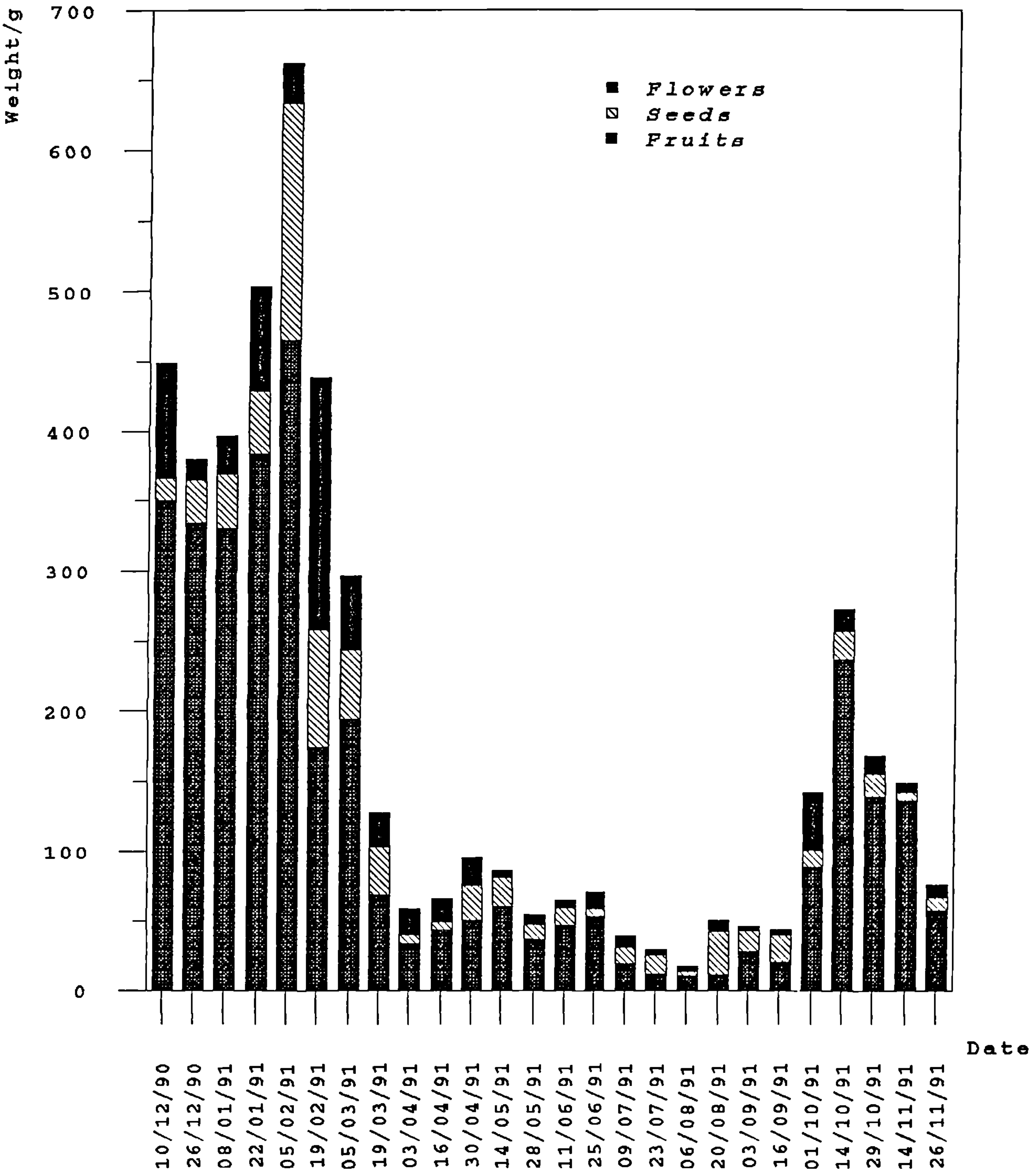


Figure 4.1 Weights of fruits, seeds and flowers collected from traps every two weeks at the IET site, December 1990 - November 1991

February, and least from March to September. Seed production was high from December to March, with a peak in February. The number of species in fruit, but not the weight, correlates with the rainfall three months previously (Pearson's product-moment correlation, coefficient 0.44, $p=0.026$). (Rainfall data are given in Appendix 3).

Sixty seven fruit species collected in traps were classified by dispersal mode. Of these, 61 were zoochorous, 5 anemochorous and only 1 autochorous. Thus, over 90% were zoochorous. The weight of zoochorous fruit collected was greatest from December to March and least from July to September. Most anemochorous fruit were collected from October to December, in February and in April; the one autochorous species collected was in December. All dispersal types show peaks of species numbers in December.

The mean weight of fruit, flowers and seeds per trap for each habitat type is shown in Figure 4.2. There was no significant difference in fruit production between BF and FH, but seed production was greater in FH ($p<0.05$).

Collections from the ground at IET (Figure 4.3) gave the highest density of flowers on the ground from December to May and of fruits between October and early April (though with an unexpected fall in January). At Gouleako (Figure 4.4), flower collection was too low to show a pattern, other than a peak in early March due to a fall of flowers of Pentadesma butyracea (Guttiferae); fruit collections were greatest from December to April. Collection of seeds from the ground showed no clear seasonal pattern at either site.

Comparing sites, the weights of fruits and seeds on the ground were significantly greater at the IET site than at Gouleako (Wilcoxon test, $p<0.005$ in both cases). Fruit available on the ground varied during the year from 76.5 kg/ha to 369.8 kg/ha at IET, and from 14.9 kg/ha to 69.9 kg/ha at Gouleako, making a five-fold difference both between sites and at each site during the year. Correlation between sites of weights collected from the ground over the year is not significant at the 5% level for fruits, flowers or seeds although fruits show a very weak trend towards correlation (Spearman's rho, $p=0.075$).

Figures 4.5 and 4.6 show the average weight of fruits, flowers and seeds per quadrat for each habitat and each collection date. There is no significant difference between FH and BF in density of fruits or seeds on the ground within either site, but IET had a significantly higher density of fruit on the ground than Gouleako in both FH and BF ($p<0.005$ and $p<0.05$ respectively), and of seeds in FH ($p<.005$).

At Gouleako, there was a significant difference in fruit density and seed density between habitats (Friedman 2-way ANOVA, $p<0.001$ and $p<0.05$ respectively). Fruit and seed densities were lowest in BAM and EUP and highest in mature FH and BF. In table 4.1, habitats are ordered according to the mean ranks given by the

Figure 4.2 Mean weight of fruits, flowers and seeds per trap collected fortnightly for each habitat at the IET site

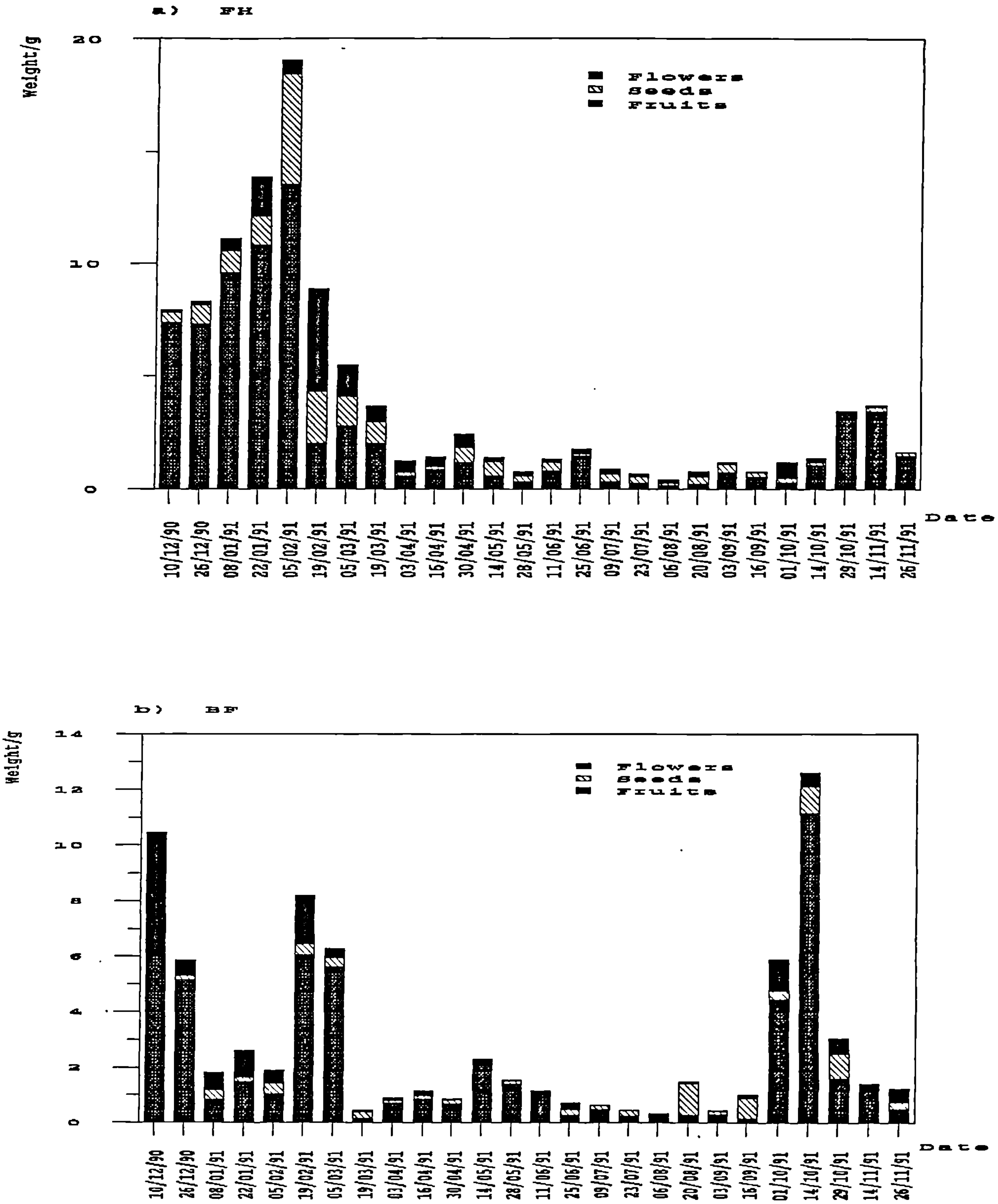


Figure 4.3 Weight of fruits, seeds and flowers collected monthly from ground quadrats at the IET site, December 1990 - November 1991

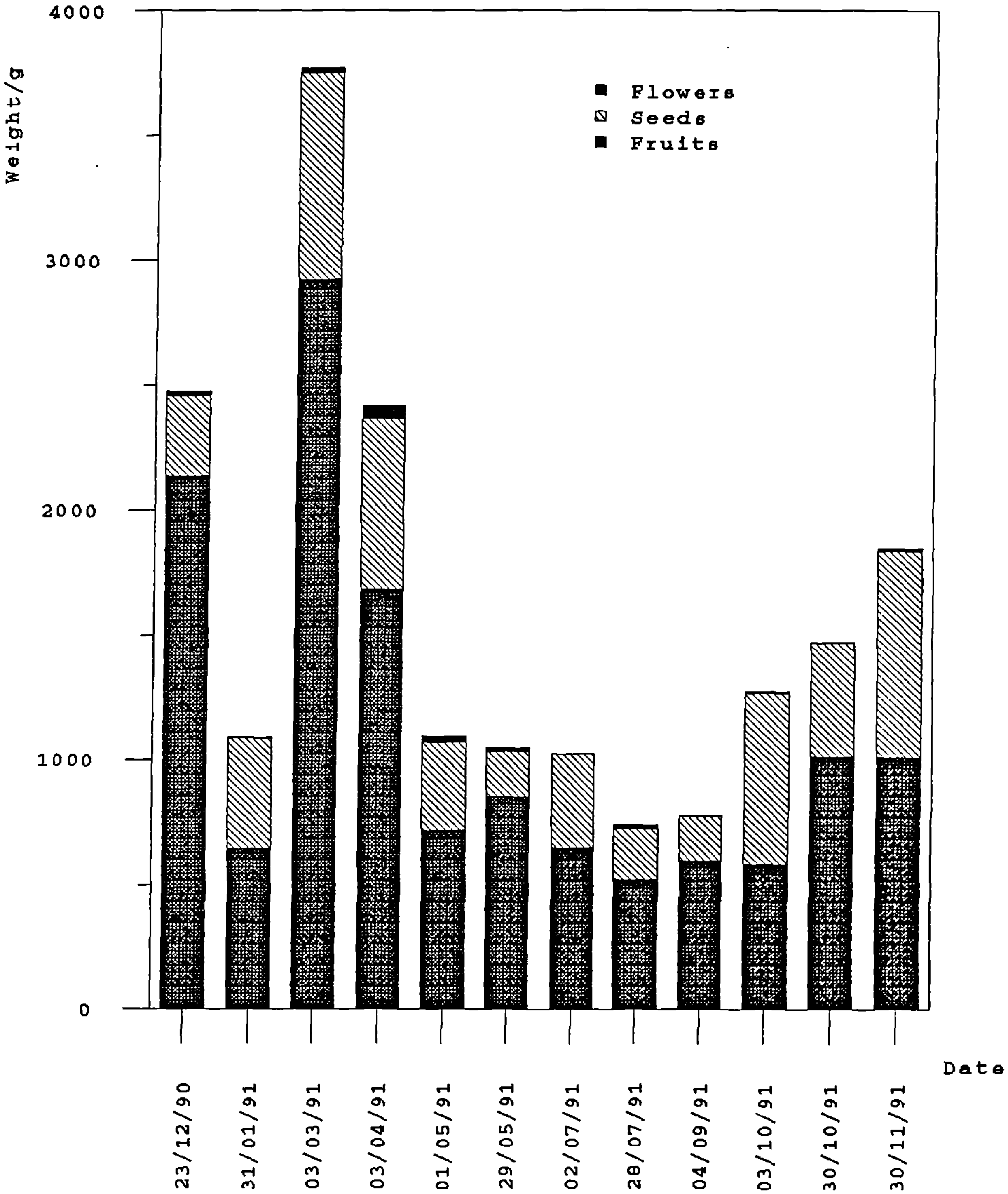


Figure 4.4 Weights of fruits, seeds and flowers collected monthly from ground quadrats at the Gouleako site, December 1990 - November 1991

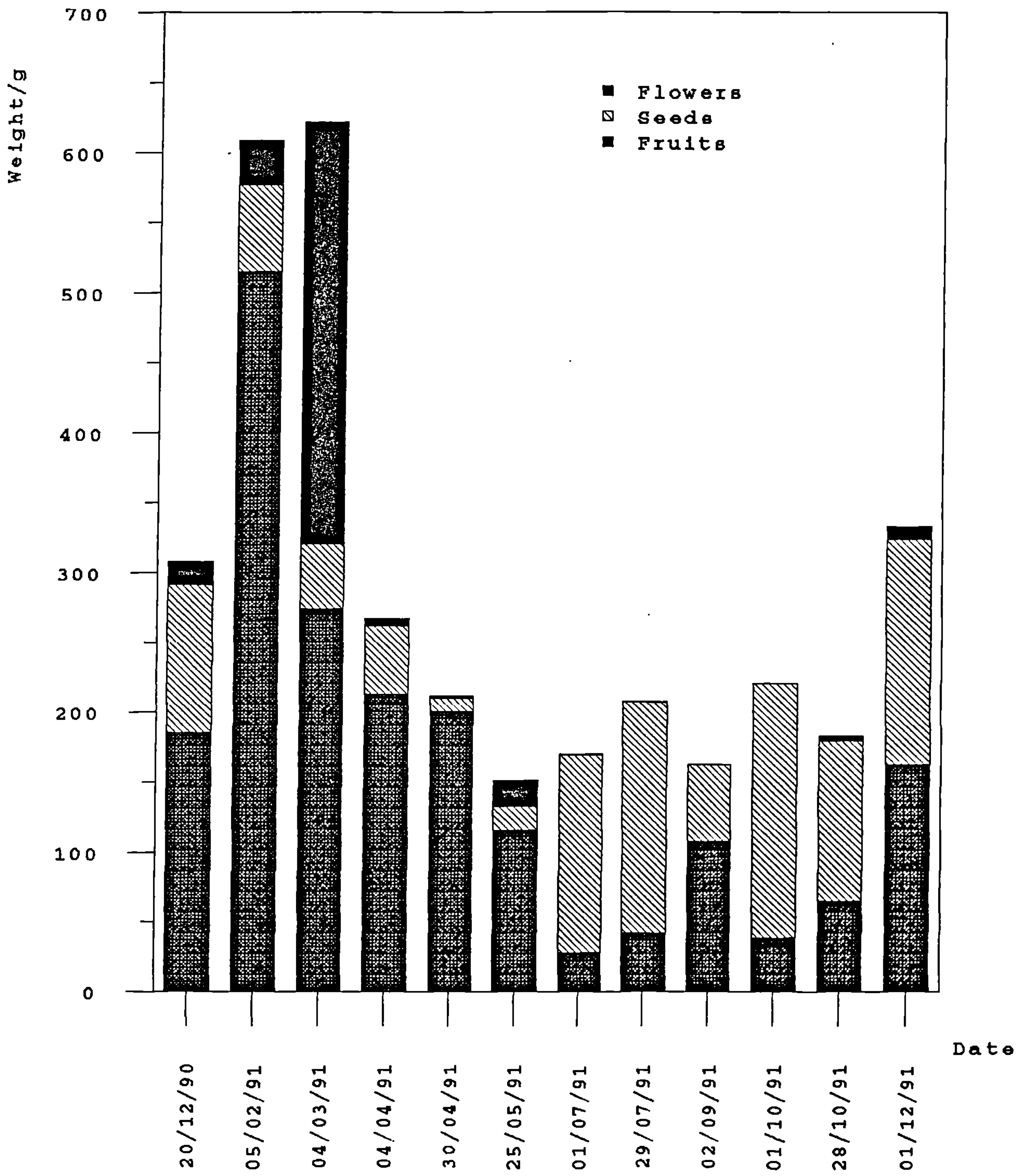
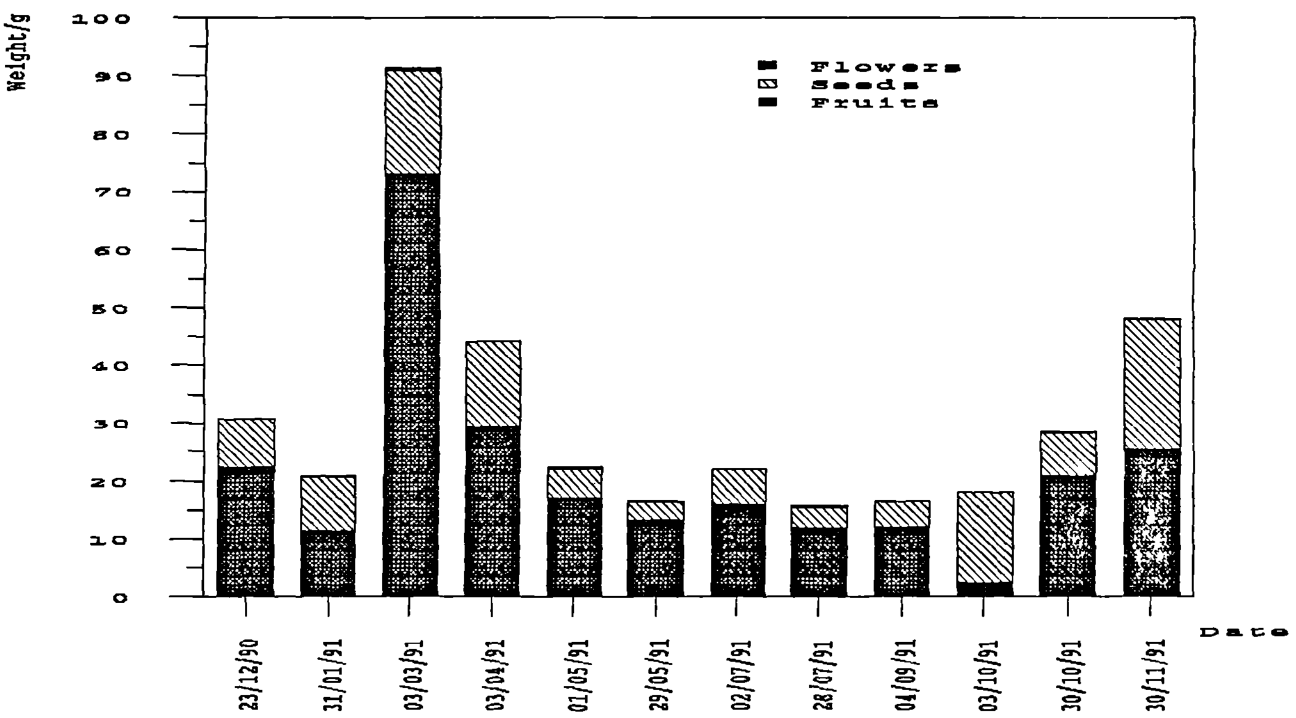


Figure 4.5 Mean monthly weight of fruits, flowers and seeds per quadrat for each habitat at the IET site

a) FH



b) BF

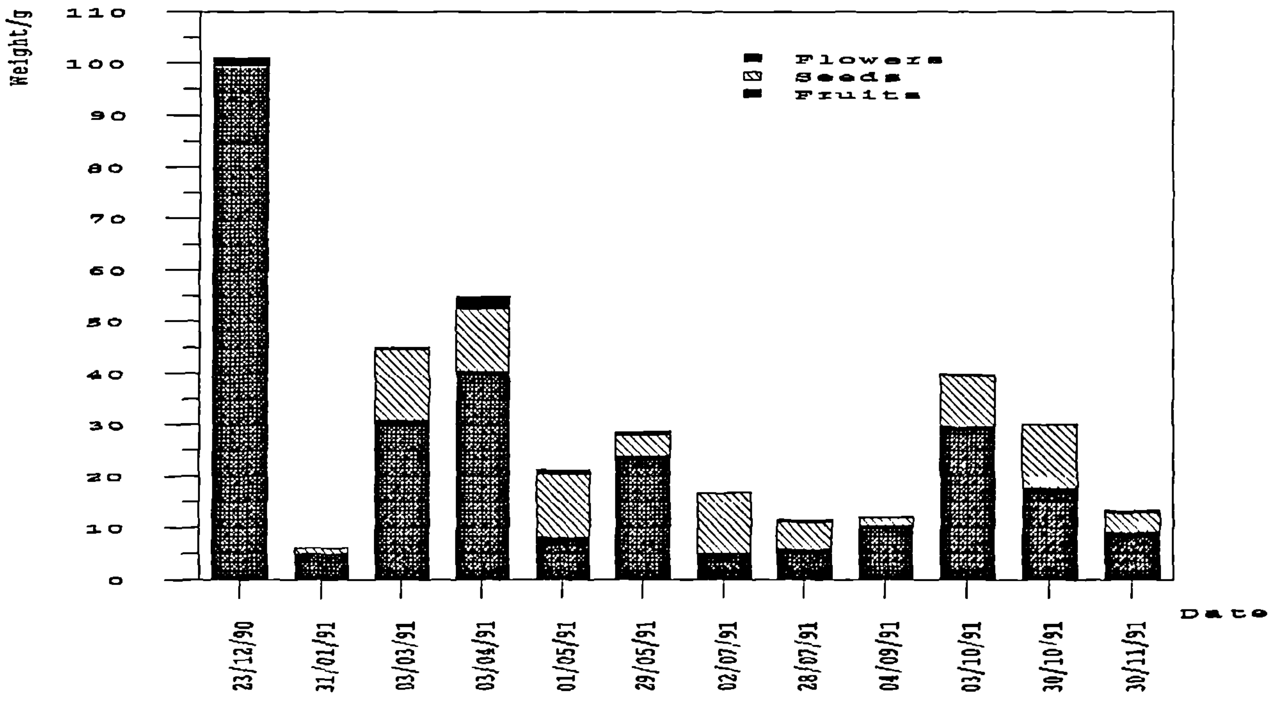


Figure 4.6 Mean monthly weight of fruits, flowers and seeds per quadrat for each habitat at the Gouleako site

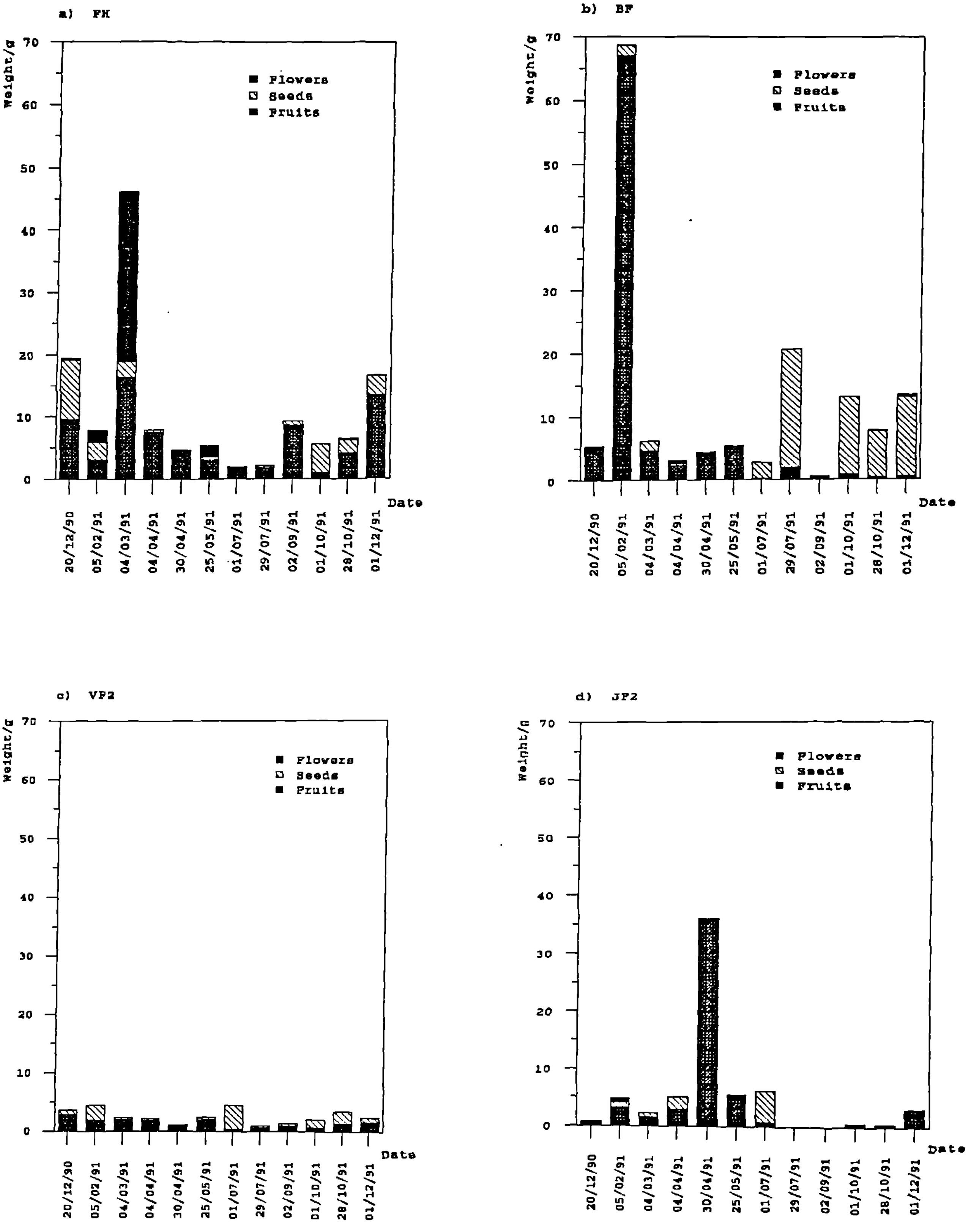
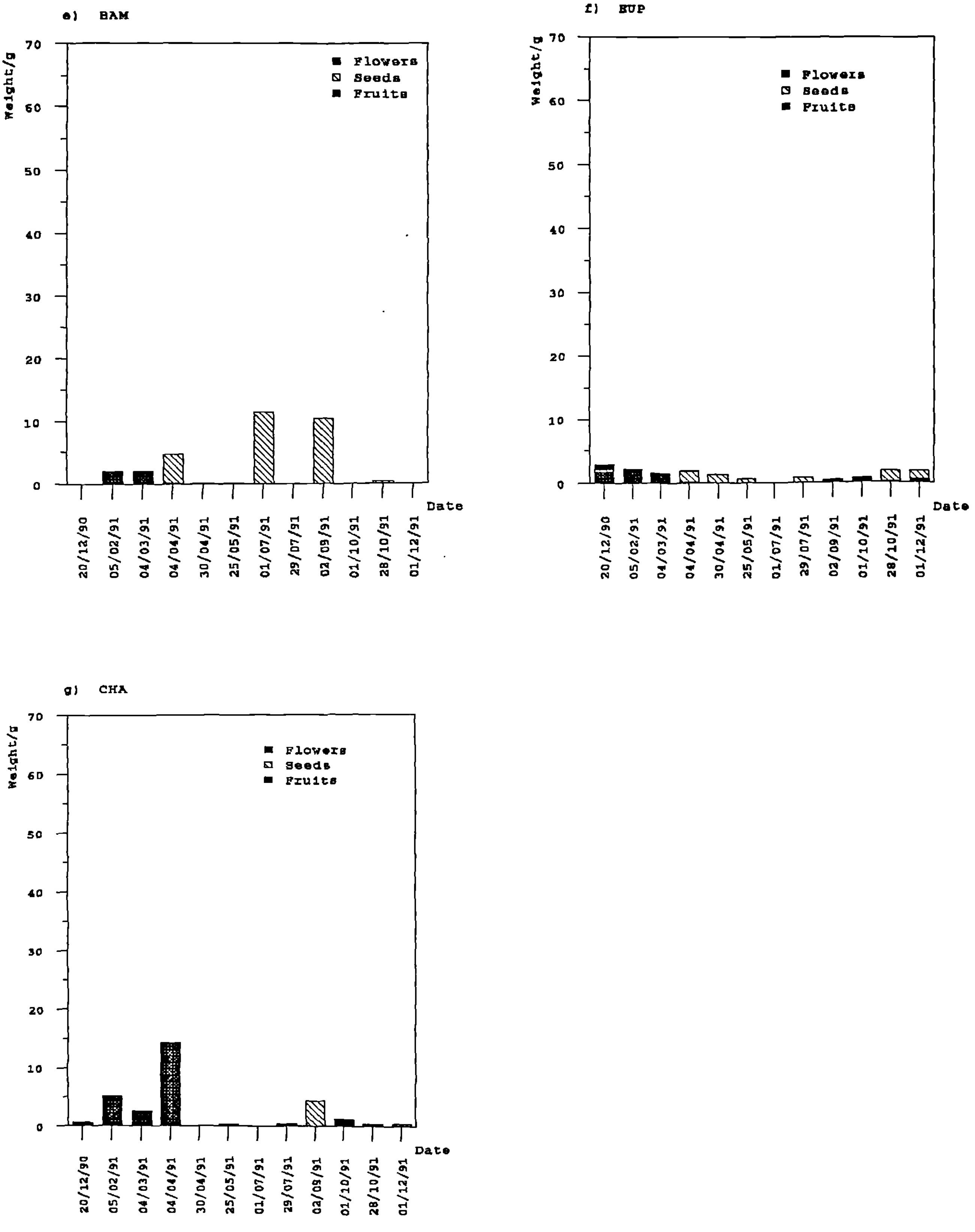


Figure 4.6 Mean monthly weight of fruits, flowers and seeds per quadrat for each habitat at the Gouleako site (cont.)



Friedman analysis, and significant differences between habitats are marked with asterisks (using the Wilcoxon test).

Table 4.1 Significant differences between habitats at Gouleako in the weight collected from ground quadrats (habitats in order of decreasing weight collected)

a) Fruits

	FH	BF	VF2	JF2	CHA	EUP	BAM
FH							
BF							
VF2	**						
JF2							
CHA							
EUP	**	**	**				
BAM	**	**	**	**	**		

b) Seeds

	FH	BF	VF2	EUP	BAM	JF2	CHA
FH							
BF							
VF2							
EUP							
BAM							
JF2							
CHA	*	*	*				

Key: * $p<0.05$ ** $p<0.005$

4.4 Discussion

In summary, the main season of flower and fruit production was during the main dry season, from December to February. Over 90% of fruit species were zoochorous; no difference in seasonality was detected between zoochorous, anemochorous and autochorous fruits. The density of fruit on the ground stayed high from December to April, the extra two months presumably reflecting the length of time that fruit remained on the ground from the February fall. High seed production coincided almost exactly with high fruit production (December to March) but seed density on the ground showed no clear seasonal pattern, suggesting that a considerable quantity of seeds remained on the ground throughout the year.

Fruit and seed densities on the ground were higher at IET than at Gouleako. This is partly because densities were lower in secondary habitats than primary forest, but in addition, IET primary forest (FH and BF) had significantly higher densities of fruit on the ground than the same habitats at Gouleako, perhaps because more mature trees had been removed at Gouleako for timber and for building materials within the village. Within secondary habitats, fruit and seed densities tended to be higher in older vegetation types (VF2, JF2) but these differences were not significant.

Neither collection from fruit traps nor collection from the ground gives an absolute measure of fruit production because of decay and predation before collection. In addition, Malenky et al (1993) found that their data from fruit traps did not correlate with measures of fruit production from surveys of trees in fruit. However, ground collections are more relevant in showing what is available at any time to ground frugivores. A comparison of results from fruit traps and from quadrats on the ground confirm that fruits and particularly seeds can remain available to ground frugivores long after their production has ceased. Thus, although collection from fruit traps shows seasonal patterns of production more clearly, collection from the ground is more appropriate for a study of food availability to ground frugivores. During the year of the present study, fruit on the ground was plentiful from December to April. Seeds, which are also an important food, remained on the ground throughout the year. Fruits and seeds were most scarce from May to September, in the short rainy and dry seasons.

Fruit trap data confirmed the findings of Alexandre (1980) that the number of species in fruit is correlated with rainfall of three months previously, and that the majority of species are zoochorous. However, like Gautier-Hion (1990), the study failed to replicate Alexandre's differences in seasonality between species with different dispersal mechanisms. The quantity of fruit produced was not clearly linked to monthly rainfall.

A recent 8-year study in Gabon (Tutin and Fernandez, 1993) suggests an alternative to rainfall as the trigger for flowering and fruiting. It was found that flowering was undelayed in years when the rains were late. Flowering seemed to be triggered not by rainfall, but by a drop in the temperature. Fruit crop size was negatively correlated with the mean daily minimum temperature of the previous dry season for all eight species tested, and in two years when this was above 21oC, most individuals failed to fruit. In the two years when there was a night below 19oC outside the dry season, individuals of all eight species flowered out of season two to four months later.

The present study was limited to a single year, and therefore cannot test such long-term patterns. However, years in which fruit crops fail are not exceptional at other sites. Foster (1982, in Smythe, 1986) estimated that fruiting patterns were severely disrupted about every ten years on Barro Colorado Island in

Panama, due to rain anomalies. Crop failures can cause massive mortality of frugivorous mammals (in Smythe, 1986). The occurrence of crop failures may be an important factor limiting the densities of frugivore populations. Only further long-term studies will determine whether this is the case in Taï.

On the shorter term, a number of studies have suggested that ranging patterns and population densities of tropical frugivores may be affected by seasonal variation in fruit availability, in particular of so-called "keystone resource" species (eg. Feer, 1988, 1989a 1989b; Fleming, 1979; Gautier-Hion and Micheloud, 1989; Smythe, 1986 Terborgh, 1986). The 5-fold fluctuation in fruit on the ground during the year recorded during the present study supports the hypothesis that there are times of relative fruit scarcity.

CHAPTER 5. DIET

5.1. Introduction

As outlined in Section 1.3, duikers are primarily frugivorous, although they also eat foliage and small quantities of flowers, fungi and animal matter. Dietary differences between sympatric species are likely to be an important factor in niche separation and reduction of competition. Moreover, fluctuating availability of food items may be a limiting factor for duiker population densities.

In this Chapter, data gathered on food eaten by duikers is presented; this is then amalgamated with data from the literature to give as full a picture as possible of duiker diets. Finally, phenological and vegetation data are used to determine the availability of known dietary items in different habitats and seasons.

5.2. Methods

5.2.1. Direct observations Observations of feeding were recorded only when the observer could clearly see what type of item was being eaten. When the duiker(s) had left the feeding site, the observer collected a sample of the food item for identification.

5.2.2. Stomach contents Stomach contents of animals killed by villagers were collected by the project workers, who stored them in plastic bags in 60% ethanol until they could be processed (always within a week). Analysis was limited to the contents of the rumino-reticulum, where unchewed food items are sometimes stored whole for several days and are therefore easy to identify. Small items may have been underestimated since they often pass straight through to the omasum (Dubost, 1984).

Each sample was washed through two sieves with different mesh sizes. Mesh size has been found to affect quantitative dietary analysis when micro-analysis of cuticular cells is used (Owaga, 1978); the smaller the mesh size, the more accurate the analysis, but the more time-consuming it is. However, for macroanalysis, sieve size makes little difference to the results (Dirschl, 1962; F. Feer (personal communication); Hart, 1985). Harding (1986, on muntjac), Hart (1985, on duikers) and Bodmer (1990, on neotropical forest ungulates) all used a 4-5 mm sieve to catch the larger items, which they suggest may represent the last meal. In this study, 4 mm and 1 mm mesh sieves were used, since it was originally intended to use the smaller fraction for microanalysis of cuticular cells, which can be used to determine species and plant parts. However, the small number of stomachs collected did not justify the time which would have been needed to build up a slide reference collection of leaves, fruit and flowers of all plant species recorded in the study sites. Therefore, the small fraction was weighed but not analyzed. The large fraction was sorted into categories (fruit, flowers, seeds, leaves and animal matter) and into species as far as possible, and all fractions were sun-dried to constant weight. The weights were recorded and the percentage of the total contributed by each fraction was calculated.

5.2.3. Information gathered from local people As samples of leaves were collected for vegetation surveys (Chapter 3), senior project workers were asked to indicate which ones they knew to be eaten by duikers. They were asked repeatedly about the same items at different times to check the consistency of their answers, and where possible, answers from different informers were compared. Local people have the opportunity to know much about duiker diets, not only from observations of eaten foliage near the fields, but also because villagers empty out the stomach contents of hunted duikers to eat the stomachs. Whole fruits and large sections of leaf are usually clearly visible in the contents.

5.3. Results

5.3.1. Direct observations Nineteen direct observations were made of duikers eating identifiable items. Eighteen of these were of *Cephalophus maxwelli*; four were of an infant, which was observed on three occasions eating dead leaves, and once eating bracket fungi. One observation was made of a juvenile Ogilby's duiker (*C. ogilbyi*) eating fruits of *Coelocaryon oxycarpum* (Myristicaceae). Of the remaining fourteen observations, nine involved fruit - *Sacoglottis gabonensis* (Humiriaceae) (four times), *Dialium aubrevillei* (Caesalpiniaceae) (three times) and *Oldfieldia africana* (Euphorbiaceae) (two times). Five involved leaves:- *Landolphia owariensis* (Apocynaceae) and *Homalium aylmeri* (Samydaceae) (once each), and unidentified species (three times). These results are shown with the dates of observations, the types of fruit and additional notes in Table 5.1.

Table 5.1 - Observations of Items Ingested by Duikers

Date	Animals observed[1]	Plant part eaten	Plant species
Cephalophus maxwelli:			
10/2/90	A ♂	fruit	Dialium aubrevillei
18/8/90	A + A	fruit	Oldfieldia africana
19/2/91	A♂ + A♀	leaves	unidentified
14/3/91	I♀	dead leaves	unidentified
29/3/91	I♀	dead leaves	unidentified
11/5/91	I♀	leaves	unidentified
12/5/91	I♀	fungi	
8/7/91	A♀	fruits	Dialium aubrevillei
8/7/91	J♀	leaves	unidentified
21/7/91	J♂ + J♀	fruits	Dialium aubrevillei
30/7/91	J♀	leaves	Homalium aylmeri
12/9/91	J♀	fruit	Sacoglottis gabonensis
15/9/91	J♂ + J♀	fruit	Sacoglottis gabonensis
26/9/91	J	fruit	Oldfieldia africana
30/9/91	2A♂'s, A♀, J♀	fruit	Sacoglottis gabonensis
5/10/91	2A♀'s	leaves	unidentified
7/10/91	2A♂'s, A♀, J♀	fruit	Sacoglottis gabonensis
20/11/91	A♀	leaves	Landolphia owariensis
C. ogilbyi:			
13/5/90	J	fruit	Coelocaryon oxycarpum

---

[1] A=Adult, J=Juvenile, I=Infant

5.3.2. Stomach contents Eleven stomachs were obtained in the course of the study - eight of C. maxwelli, two of C. dorsalis and one of C. ogilbyi. Table 5.2 shows details of the samples obtained together with the percentage dry weight of each sample which was made up of each type of food item.

Table 5.2 - Stomach samples obtained with % dry weight of fruits, seeds, leaves and other items making up the large fraction (>4 mm)

Date	Species	Total dry weight /grams (Weight of large fraction in brackets)	Percentage weight of large fraction from each type of food item		
			Fruits & seeds	Vegetative parts	Other
9/5/90	C.max	122 (104)	86	4	10 (worm)
15/5/90	C.max	58 (34)	44	50	6 (flowers)
28/11/90	C.max	74 (60)	98	2	
28/11/90	C.max	74 (41)	100	0	
18/12/90	C.dors	88 (54)	98	2	
24/2/91	C.max	55 (42)	100	0	
13/3/91	C.ogil	167 (119)	92	7	1 (flowers)
18/5/91	C.max	99 (89)	89	10	1 (flowers)
10/7/91	C.max	100 (58)	98	2	
?/8/91	C.dors	116 (79)	85	15	
31/8/91	C.max	29 (4)	0	75	25 (flowers)

Ten of the eleven stomachs contained fruit and seeds, nine contained vegetative parts, and four contained flowers. The only animal matter found was a single worm in stomach 1.

Fruit and seeds formed at least 85% of the total dry weight in nine stomachs; during the season of greatest fruit abundance this figure was over 90% for all samples, whereas from May to August this was only the case in one sample, and a greater weight of leaves and flowers was found. Thus, there is some evidence that in the season when fruit is most scarce, the diet includes more leaves and flowers.

The species of fruits found in the stomachs are summarised in Table 5.3; full details of the contents of each stomach are given, with their dry weights, in Appendix 7.

A total of 35 species of fruits and seeds were recorded overall, of which twenty five were identified. Of these, one occurred in five samples (Dialium aubrevillei, Caesalpiniaceae); one occurred in four samples (Nauclea sp., Rubiaceae); and four occurred in three samples (Amphimas pterocarpoides, Caesalpiniaceae; Chrysophyllum taiense, Sapotaceae; Dacryodes klaineana, Burseraceae, and Diospyros sp., Ebenaceae). Most species were from trees, and all except three species were either fleshy fruits (drupes, berries or composite fruits such as figs) or seeds from leguminous pods. The two additional fruits which were seen being eaten (Sacoglottis gabonensis, Humiriaceae and Oldfieldia africana, Euphorbiaceae) were also fleshy fruits from trees.

Table 5.3 - Fruit and seed species recorded in duiker stomach contents

Species	Fr.	Form	Stomachs[1]	IU[2]
Dialium aubrevillei	fs	a	6,7,8,9,10	16.22
Pseudospondias microcarpa	fs	a	1	10.82
Diospyros sp. (seeds only)	fs	a	6,7,8,9	6.17
Jaundea pinnata	fs	l	3	4.79
Amphimas pterocarpoides (seeds only)	pl	a	6,7,8	3.93
Chrysophyllum pruniforme	fs	a	4,6	3.61
Sp. 158 (Connaraceae)	fs	l	4,5	3.35
Scytopetalum tieghemii	fs	a	2	3.31
Hugonia afzelii	fs	s	3,4	3.30
Xylia evansii (seeds only)	p?	a	3	2.92
Chrysophyllum taiense	fs	a	4,6,10	2.41
Cola lateritia	fl	a	6,7	2.38
Nauclea sp.	fm	a	3,6,8,10	2.32
Bussea occidentalis (seeds only)	pl	a	6	1.49
Scottelia chevalieri	cs	a	8	1.12
Combretum paniculata	cs	a	2	<1
Tetrorchidium didymostemon	cs	s	2	<1
Memecylon guineense	fs	a	2	<1
Gilbertiodendron splendidum (seeds only)	pl	a	2	<1
Pycnanthus angolensis (seeds only)	fs	a	2	<1
Ficus vogeliana	fs	a	3	<1
Dacryodes klaineana	fs	a	4,5,6	<1
Anthonotha fragrans (seeds only)	pl	a	6	<1
Parkia bicolor	fm	a	6,7	<1
Coelocaryon oxycarpum	fm	a	8	<1
Thaumatococcus daniellii	fm	h	10	-

Key: Fruit types: f=fleshy, p=pod, c=capsule, a=achene;
s=small (<3 cm); m=medium (3-5 cm); l=large (>5 cm)
Growth form: a=tree, s=shrub, l=liane, h=herb

[1] All stomachs are of *C. maxwelli* except 5 and 10 (*C. dorsalis*) and 8 (*C. ogilbyi*)

[2] IU=Index of utility (mean % dry weight per stomach x % occurrence. See text below). Calculated for *C. maxwelli* only.

For _C. maxwelli_, an average of 5.6 species of fruit and seeds were found in each stomach (range 0 - 11). The Index of Utility (IU, after Dubost, 1984; Feer, 1988, and Hart (1985)) was calculated for each species as follows:-

IU = Mean % dry weight per stomach x % of stomachs in which species occurred.

Only two species (_Dialium aubrevillei_, Caesalpiniaceae and _Pseudospondias microcarpa_, Meliaceae) contributed more than 10% of the total IU.

5.3.3. Information gathered from local people The leaves of 40 species of plants were consistently reported to be eaten by duikers by the senior local assistants. These could not be tested during the present study but since there is an almost total lack of information on leaf species eaten by duikers, they are listed in Appendix 7.2 as a starting-point for future research.

5.4. Discussion

5.4.1. Diets Duiker diets have been studied in detail in Gabon (Dubost, 1984; Feer, 1988, 1989b) and in Ituri, Zaïre (Hart, 1985). Dubost (1984) gives the mean percent dry stomach weight of fruit and seeds, flowers, vegetative parts (leaves and stems), fungi and animal matter for the six species of duiker present (_Cephalophus callipygus_, _C. dorsalis_, _C. leucogaster_, _C. monticola_, _C. nigrifrons_ and _C. sylvicultor_) and the water chevrotain (_Hyemoschus aquaticus_). For all species, fruit and seeds accounted for over 68% of the total. Vegetative parts (mostly stems and dead leaves) accounted for 20 - 31 % in all species except _Cephalophus_ callipygus (16%). Fruits, seeds and leaves were present in all stomach samples. Flowers, fungi and animal matter were not always present and between them accounted for no more than 3% of the total. Feer (1988, 1989b) worked more intensively on C. callipygus and C. dorsalis and found their diets to be 90% fruit, 8% vegetative parts and 86% fruit, 11% vegetative parts respectively. Hart (1985) found that fruits and seeds made up 80 - 97% of total dry weight for the same seven species; vegetative parts (which were mostly young leaves fallen from canopy trees, and dead leaves) averaged less than 12% in all species except C. nigrifrons, and were completely absent from some samples. In the present study, vegetative parts contributed a mean of 15% of total dry weight. This figure was below 10% for all samples taken during the period of fruit abundance, and ranged up to 75% outside this period. Both Feer and Hart also report an increase in the proportion of leaves in times of fruit scarcity; Hart found that at this time, the diet of C. monticola became dominated by foliage, which normally accounted for less than 5% of the total.

Most other less detailed studies confirm this picture. Kranz and Lumpkin (1982) examined four stomachs of C. sylvicultor and found that fruit made up 71.3% dry matter, and leaves 28.6%. Ralls (1973) describes C. maxwelli as primarily a browser, with fruit forming an important part of the diet. In contrast, Henle and Apfelbach (1985) observed feeding by four rehabilitated C. dorsalis in Côte d'Ivoire and reported a diet of only 26.7% fruit; however, this discrepant result is almost certainly due to the different method of data collection.

In most studies, only fruits and seeds eaten have been identified to species level. Although the mean number of species per stomach is low (4 - 9, Dubost (1984); 8, Feer (1988); 4 - 7.5, Hart (1985)), a very wide range of food species has been found for each species of duiker. Feer (1988, 1989b) found 110 food species in 68 C. callipygus stomachs, and 98 in the same number of C. dorsalis stomachs; the number of species was still increasing with this sample size. Hart (1985) found over 240 species in 191 stomachs of seven species of ruminant. In the present study, an average of 5.6 species of fruits and seeds were found per stomach. With a sample of only eight stomachs of C. maxwelli, 35 species of fruit were recorded.

Dubost, Hart and Feer all calculated an index of utility (IU) to identify the most important fruit species in the diet, and found that just a few key species made up most of the food consumed. Dubost (1984) found that each ungulate species had 3-7 "preferred" species (contributing over 5% of the total IU); Feer (1988) found that just one species, Dacryodes buettneri (Burseraceae), made up over 50% of the total IU for both C. callipygus and C. dorsalis, and only 13% of species eaten contributed over 1%. Hart (1985) found that for most stomachs, just two food species gave at least 67% of the total dry weight of contents. In this study, only two species of fruit or seed contributed more than 10% of the total IU. These were Dialium aubrevillei (Caesalpiniaceae) and Pseudospondias microcarpa (Meliaceae), and their predominance in diet analysis is compared below with their abundance in the two study sites.

It has been shown that most fruits and seeds eaten were fleshy fruits or leguminous seeds; Feer (1988) also found that most fruits eaten were drupes or berries and seeds were from drupes, berries or pods. However, duikers eat a wide range of fruit and seed species and it is unclear whether they forage preferentially for certain fruit types or simply eat what is most abundant. Dubost (1984) found that different fruit species were eaten in proportion to the numbers available on the ground, and therefore according to the probability of encountering them (only the larger consumer species consumed fruits in proportion to their weight on the ground as well as their number). Gautier-Hion et al (1985a) looked at a number of characteristics of fruits eaten by the frugivorous community in forest near Makokou, and found that ruminants did not select for fruit type, colour, or nutrient content; the majority of fruit species eaten were fleshy and brown or yellow, but these were also the most commonly available. In the present study, 82% of the total dry weight of fruits collected was made up of fleshy fruits. Thus the predominance of fleshy fruits in the diet reflects their predominance in the environment.

The only selection criterion found to be valid by Gautier-Hion et al was fruit size - small ruminants eat smaller items than large ruminants. Hart (1985) also found this to be the case, and in addition found that larger species eat more mature fruits while smaller species eat more immature fruits and seeds. Of the fruits recorded in the present study in stomach contents of C. maxwelli, 14 species were less than 3cm in diameter; 7 were soft fruits 3-5 cm in diameter; and one was soft and over 5 cm in diameter. Seeds of larger leguminous pods were also recorded. All fruits less than 3cm diameter were found whole, whereas larger fruits were found only in fragments; this suggests the maximum size of items which can be swallowed is about 3cm in diameter. The largest fruit recorded, Cola lateritia (Sterculiaceae) has a hard skin covering a sweet jelly encasing the seeds. A captive black duiker had much difficulty in breaking it open, but then consumed the jelly, seeds and husk with enthusiasm. Fragments of husk and seeds were found in a stomach of C. ogilbyi, which is of comparable size to C. niger; only the seeds were found in the smaller C. maxwelli, which would probably be unable to break open the husk and would be reliant on finding fragments of the fruit left by other frugivores. One other fruit over 3cm diameter (Sacoglottis gabonensis, Humiriaceae) was several times seen to be eaten, although it was not recorded in stomach contents. This fruit had a very soft pulp when ripe, and duikers chewed the pulp off the seed rather than eating the fruit whole (personal observation). Mashed-up pulp of larger fruits may wash away or remain unnoticed during analysis of stomach contents; only microanalysis by identification of plant cuticle cells would lessen this inaccuracy.

Thus, food items available to C. maxwelli included fruits, seeds and flowers under 3cm diameter; larger fruits which are soft enough for flesh to be chewed off (which may be under-represented in stomach analyses); seeds of dehiscent pods; and fragments of large, hard fruits which have been opened and dropped by other frugivores such as primates.

Hart (1985) undertook chemical analyses of some commonly eaten fruits and succeeded in finding additional selection criteria related to their nutritional content, both from food choice tests with captive animals and from stomach analyses of wild animals. Choice tests with captive animals showed preferences for fruits which had a high dry matter yield and a high ratio of protein to fibre and condensed tannin content. All species of duiker showed selectivity in food selection in the wild, with 40 - 83% of fruit species being actively avoided, and many preferred species being uncommon. However, although some fruit species were consistently avoided, others were preferred at some sample times and avoided at others. It is probable that selectivity varied with fruit abundance. The smallest species, C. monticola, was the most selective of high quality items, while C. dorsalis was the least selective. Below, dietary preferences are compared with phenology data and tree survey data to further assess selectivity of food items at Taï.

5.4.2. Comparison with data from phenology studies and tree surveys Looking at the ten commonest food items recorded on the ground in phenology studies for each site (see section 4.3), we find that they include only two fruits which are less than 3cm in diameter. These are two of the three highest contributors to the total IU in C. maxwelli stomach contents (Dialium aubrevillei, Caesalpiniaceae (IU = 16.22), and Diospyros sp., Ebenaceae (IU = 6.17)). Three others of the commonest fruits were over 3cm diameter but soft (Sacoglottis gabonensis (Humiriaceae), Parinari excelsa (Chrysobalanaceae) and Pentadesma butyracea (Guttiferae)); observations of a captive black duiker (C. niger) revealed that these were chewed before the soft pulp was swallowed, so they may have been missed in the stomach analysis. *S. gabonensis* was seen to be eaten by *C. maxwelli* in the field. *Klainedoxa gabonensis* (Simaroubaraceae) fruits were too hard to be opened by the black duiker, although they were eaten enthusiastically if broken into pieces by the keeper; thus, the smaller *C. maxwelli* would also be unable to open them. *Ricinodendron heudelottii* (Euphorbiaceae) fruits were the most common species in collections at Gouleako; other studies have found that they are eaten by medium and large-size duikers but could not be opened by smaller species such as *C. monticola* (Dubost, 1984; Feer, 1988; Hart, 1985). They were not recorded in this study in the diet of *C. maxwelli*.

The five fruits under 3cm diameter which contribute the greatest weight over the year in the two study sites are given below:

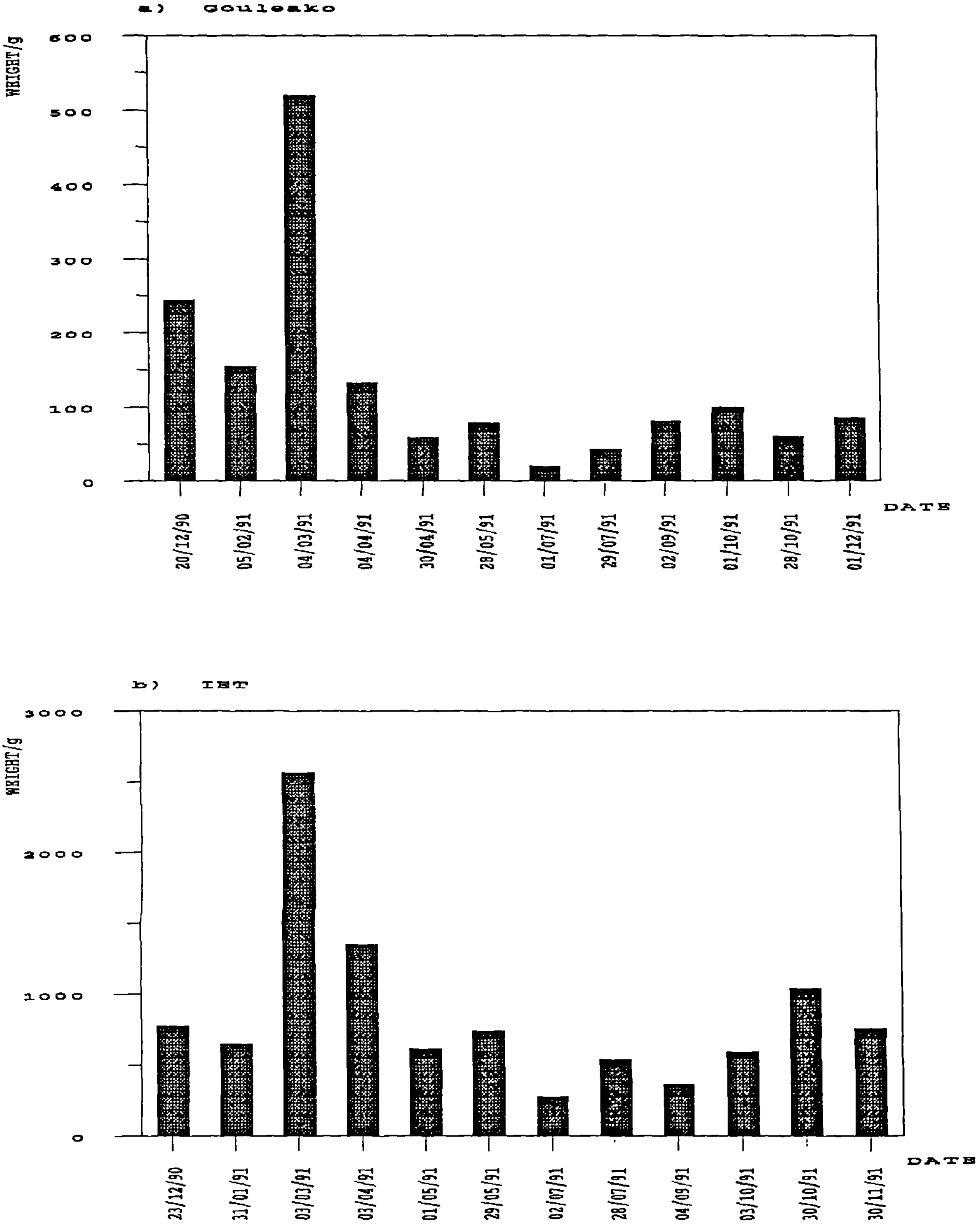
IET: *Diospyros sanzaminika* (Ebenaceae)
Dialium aubrevillei (Caesalpiniaceae)
Diospyros mannii (Ebenaceae)
Combretum/Combretodendron sp. (Combretaceae)
Chrysophyllum taiensis (Sapotaceae)
GOULEAKO: *Dialium aubrevillei* (Caesalpiniaceae)
Combretum/Combretodendron sp. (Combretaceae)
Harungana madagascariensis (Guttiferae)
Diospyros sanzaminika (Ebenaceae)
Oldfieldia africana (Euphorbiaceae)

All of these were recorded as eaten by *C. maxwelli* except *Harungana madagascariensis*, which is a small berry of a shrub in secondary vegetation, collected in eight months of the year. *Oldfieldia africana* was seen being eaten but was not found in stomach contents; the winged fruits of *Combretum*/*Combretodendron* were found in only one stomach, in spite of being the second greatest contributor to the weight of fruit collected at Gouleako and the fifth greatest at IET.

Thus there is a suggestion of selectivity even amongst small fruits which can be swallowed whole. *Pseudospondias microcarpa* (Meliaceae), was the second highest contributor to the total IU because of its very large percentage contribution to one stomach sample, but it is likely to have been a rare food item. The species was recorded only once during tree surveys.

Using the phenology data from Chapter 4, it is possible to look again at seasonal availability of food. Figure 5.1 shows the weight collected each month at each site of potential food items - fruits, flowers and seeds that are neither too large nor too hard for consumption by *C. maxwelli*. These include all flowers; fruits and seeds under 3cm diameter; larger fruits which are soft (but not single, large seeds from such fruits); and seeds from dehiscent pods. The pattern of seasonality is unchanged from that for the total collections; food is relatively abundant from October to March, with a peak in February, and relatively scarce in April to August, with a low in June. In the season of scarcity in 1991, most of the available mass of fruits at IET was made up of *Parinari excelsa*, *Sacoglottis gabonensis*, *Dialium aubrevillei* and *Coelocaryon oxycarpum*; at Gouleako, fruit collection was very low (22 g from 102 m^2 in June), and was made up of small quantities of *Harungana madagascariensis*, *Diospyros* spp., *Pentadesma butyracea*, *Dialium aubrevillei*, *Parinari excelsa*, and *Nauclea* sp. Stomach samples from this season contained all the small fruits amongst these species except *Harungana madagascariensis*, and also fragments of the larger species *Coelocaryon oxycarpum* and *Nauclea* sp. (see Appendix 7.1);

Figure 5.1 Weights of potential food items collected each month from ground quadrats



animals were also seen eating Sacoglottis gabonensis Most of these fruits were found throughout much of the year, but were available in smaller quantities at this time. Four of the six stomach samples collected at this time of year had a large percentage of leaf matter (Table 5.2), which is an additional indicator that fruits were in short supply.

Turning again to data from Chapter 4, we can reassess differences in food abundance between habitats by recalculating mean monthly densities for fruit and seeds using only potential food items. The IET site still had a significantly greater density of these fruits and seeds on the ground than the Gouleako site (Wilcoxon test, $p < 0.05$) and this difference was still found when only mature forest at the two sites was compared (IET FH against Gouleako FH and IET BF against Gouleako BF, Wilcoxon tests, both $p < 0.05$). Data from tree surveys (Chapter 3) show that mature forest in Gouleako had a lower proportion of some species important in duiker diets, including Scytopetalum tieghemii (Scytopetalaceae), Diospyros spp. (Ebenaceae) and Sacoglottis gabonensis (Humiriaceae). The first of these is used for building by villagers. Diospyros spp. are the ebonies, which are harvested during logging, along with other potential food species such as Tarrietia utilis (Sterculiaceae).

There was also a significantly greater density of edible items in FH than BF for both sites (Wilcoxon test, $p<0.05$). Tree survey data show that Diospyros spp., Dialium aubrevillei and Chrysophyllum taiense were all more common in FH than BF. On the other hand, Sacoglottis gabonensis was more often recorded in BF than FH.

In secondary vegetation, trees which have reached fruiting age are relatively scarce. The younger vegetation types at Gouleako had a lower density of fruits and seeds than the older types (Section 4.3). There were also significantly different densities of food items in the five secondary habitats at Gouleako (Friedman 2-way ANOVA, $p<0.005$). Table 5.4 orders all habitats at Gouleako by descending mean rank density and shows significant differences between pairs of habitats (using the Wilcoxon test). Bamboo had the lowest density of potential food; it also had the lowest density of trees.

Table 5.4 Significant differences between secondary habitats at Gouleako in the density of potential food items collected in ground quadrats

	GFH	GBF	VF2	CHA	JF2	EUP
GBF	*					
VF2	**	ns				
CHA	**	ns	*			
JF2	**	ns	ns	ns		
EUP	**	**	*	ns	ns	
BAM	**	**	*	ns	ns	ns

Key: * $p<0.05$ ** $P<0.005$

The species of potentially edible fruits, seeds and flowers which contribute more than 5% of the total density for each habitat in each site are given below in order of density. JBF was excluded from the analysis due to an insufficient sample size, but data on vegetation show that predominant trees include Macaranga spp. (Euphorbiaceae), Tetrorchidium didymostemon (Euphorbiaceae) and Harungana madagascariensis (Guttiferae).

IET FH - Parinari excelsa (Chrysobalanaceae), Sacoglottis gabonensis (Humiriaceae), Diospyros sanzaminika (Ebenaceae), Dialium aubrevillei (Caesalpiniaceae), Rhaphiostylis cordifolia (Icacinaceae)
IET BF - Sacoglottis gabonensis (Humiriaceae), Diospyros sanzaminika (Ebenaceae), Parinari excelsa (Chrysobalanaceae), Licania elaesperma (Rosaceae), Coelocaryon oxycarpum (Myristicaceae)
GOU FH - Pentadesma butyracea (Guttiferae), Dialium aubrevillei (Caesalpiniaceae), Combretum/Combretodendron spp. (Combretaceae), Trycoscypha arborea (Anacardiaceae), Sacoglottis gabonensis (Humiriaceae)
GOU BF - Nauclea sp. (Rubiaceae), Oldfieldia africana (Euphorbiaceae), Uapaca guineensis (Euphorbiaceae), Dacryodes klaineana (Burseraceae)
GOU VF2 - Diospyros sanzaminika (Ebenaceae), Pentaclethra macrophylla (Mimosaceae), Harungana madagascariensis (Guttiferae), Combretum/Combretodendron spp. (Combretaceae), Dialium aubrevillei (Caesalpiniaceae), Anthonotha fragrans (Caesalpiniaceae)
GOU JF2 - Combretum/Combretodendron spp. (Combretaceae), Harungana madagascariensis (Guttiferae), Diospyros sanzaminika (Ebenaceae)
GOU EUP - Harungana madagascariensis (Guttiferae), Ficus capensis (Moraceae)
GOU CHA - Diospyros sanzaminika (Ebenaceae), Combretum/Combretodendron spp. (Combretaceae), Momordica charantia (Cucurbitaceae)
GOU BAM - Triplochiton scleroxylon (Sterculiaceae)

5.5. Conclusions

In summary, it has been shown that C. maxwelli eat primarily fruit, but the proportion of leaves and flowers increases in the season when fruit is scarce. Fruits eaten are limited to those which are under 3 cm in diameter (which can be swallowed whole), or fruits which are soft enough to break off pieces of pulp. Seeds from leguminous fruits are also eaten. Larger, tougher fruits may be eaten when fragments dropped by other frugivores are found.

Within these limitations, duikers have wide tastes and will eat most fruits which are available, although there is some evidence for the selection of preferred fruit species. Potentially edible species were most plentiful in the main dry season (November to

March) and most scarce in the short rainy and dry seasons (April to August), when a number of species were still in fruit but were producing only very low amounts. Providentially, this is a time when seedlings and young shoots are plentiful. Looking at different vegetation types, FH had a more abundant crop of potential food species than BF, and mature vegetation types had more fruit than younger secondary vegetation. The mature forest at IET had far more fruit than the more disturbed mature forest at Gouleako; in the latter, most of the large trees had been cut for timber and domestic use.

This initial study of the diet of C. maxwelli shows that extensive further research is needed to understand the role of dietary specialisation in reducing interspecific competition, and the part played by fruiting patterns in limiting populations. It is already clear that physical constraints on ingestion of food allow for dietary divergence between duiker species of differing body size; C. maxwelli, the smallest duiker species in Taï, is the most constrained. Food selectivity in grazers and browsers has been related to incisor breadth and body size (eg. Gordon and Illius, 1988), but in frugivores which eat many fruits whole, throat size is more relevant to the size of items selected. These aspects can best be defined by studies of jaw structure and captive feeding trials. Nutritional content of food items is likely to be the next most important factor in dietary selection, and more information is needed on the nutritional content of both fruits and leaves before this can be assessed. Research could begin from fruits recorded in diets in this study and the list of leaves in Appendix 7.2 and could be developed alongside food choice tests with captive animals. Lastly, a far larger number of stomach content samples from wild animals will give a much fuller picture of natural diets and help to direct captive studies.

CHAPTER 6. THE USE OF SPACE BY Cephalophus maxwelli

6.1. Introduction

Maxwell's duiker (C. maxwelli) is the most common species of duiker in Taï and was the focus of a more detailed study which will be described in the next two chapters. Our knowledge of its ecology is limited since it has not been studied intensively in the wild, but the reports available suggest that it lives solitarily or in pairs (Aeschlimann, 1963; Baudenon, 1958) and that it shows a preference for edge habitats (Ralls, 1973; Baudenon, 1958) and dense secondary thickets (Aeschlimann, 1963). Its ecology and social system have often been assumed to be similar to that of its closest relative, C. monticola (see Section 1.3 and Ralls, 1973), which lives in monogamous family groups in small defended territories (mean size 2.5 to 4 ha (Dubost, 1980) or 3.4 to 6.4 ha (Hart, 1984)). However, C. maxwelli is considerably larger than C. monticola (Body weights 8 to 11 kg and 4 to 5.5 kg respectively) and may use different ecological strategies from the latter species. It is also likely to have a proportionately larger home range (Harestad and Bunnel, 1979).

In this chapter, results are presented on the ranging and habitat preferences of C. maxwelli, which were studied following the attachment of radio-collars to ten individuals. The methods of capture and the radio equipment used are described in Chapter 2. In the discussion these factors are related to characteristics of the vegetation and availability of fruit, as described in Chapters 4 and 5. In Chapter 7, data are presented on various aspects of behaviour of C. maxwelli.

6.2. Methods

Radio-tracking was used to determine the movements of each duiker. As precise pinpointing by triangulation was not possible and direct observations were difficult (see sections 2.5 and 2.6), radio-tracking was used to locate animals to the nearest grid-cell. After homing in on the radio-signal, the transects on at least two sides of the cell were walked whilst listening frequently to the signal to check its direction. Grid-cells were defined in the field by the position of the transects and were mostly about one ha in size. At Gouleako, they were defined additionally by observable habitat boundaries where possible. The reliability of locations determined in this way proved good when radio-signals were used to approach within sight of animals or to capture them, and the method caused less disturbance than repeated visual contact (see section 2.6).

Successive locations for each animal were at intervals of 1.5 to 2 hours. Since all home ranges were less than 400 m across, and could be crossed by a duiker in less than 15 minutes, the long time interval made it likely that successive locations were time-independent. In addition, this time interval allowed up to four animals to be followed at once.

Since Maxwell's duikers were found to be diurnal (see Chapter 7), location data were balanced throughout the day for 2-hour intervals from 0630 to 1830 and were collected for each duiker in each season, until additional data points added no new locations to the cumulative range.

Additional estimates of home range sizes over the whole study period were made from sighting data, which were analyzed by the minimum convex polygon method (described in Kenward, 1987, p. 170). An estimate from sighting data was not possible for the juvenile female Gabrielle, as data were insufficient.

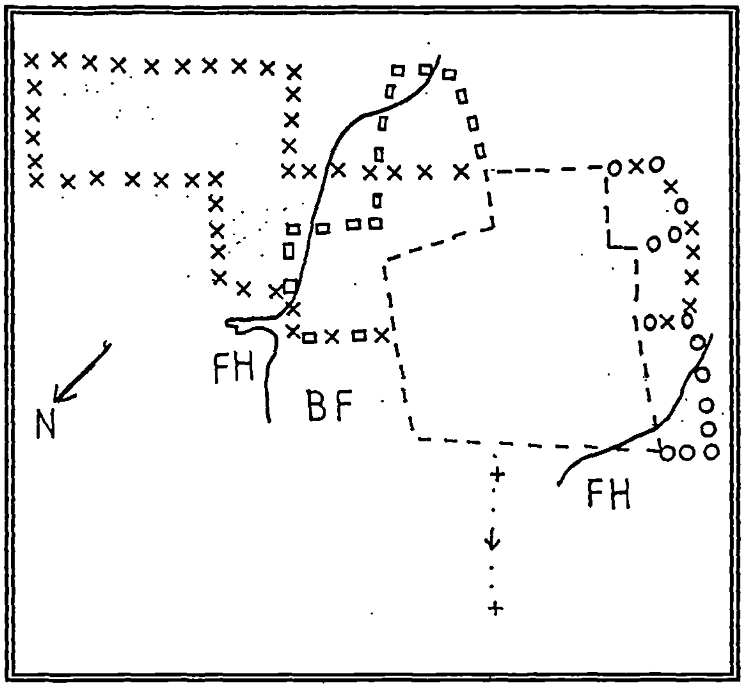
6.3. Results

6.3.1. Home range size

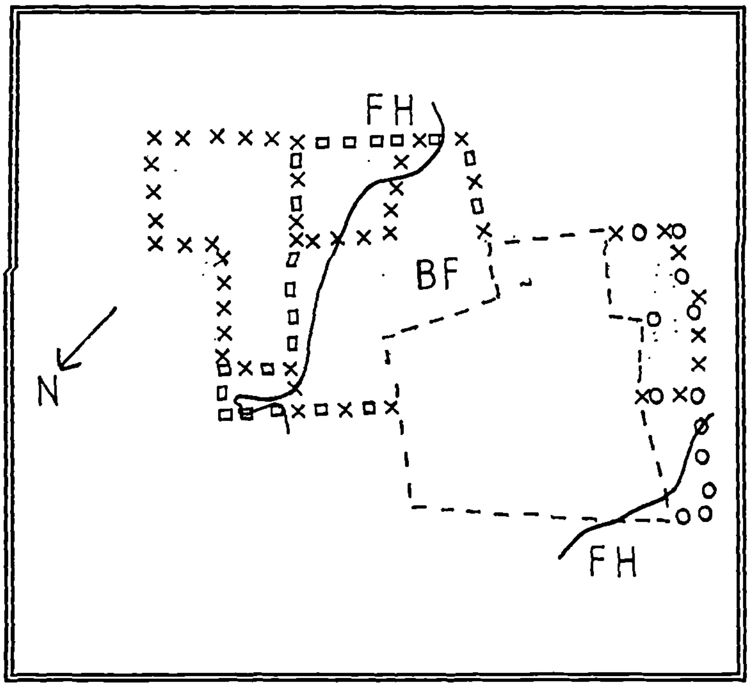
6.3.1.1. IET Seasonal and total home range sizes of duikers at IET are presented in Table 6.1 and Figures 6.1 (from radio-tracking data) and 6.2 (from sighting data). Ranges were determined during the main dry season (December 1990 to March 1991), the short wet season (May to July 1991) and the main wet season (September to November 1991). All figures in Table 6.1 are from radio-tracking data except those in parentheses in the last column, which are from sighting data. Four of the six *individuals* tracked made occasional expeditions well outside their normal ranges and these expeditions are dealt with separately (section 6.3.3).

Overall range sizes by grid-cell analysis varied between individuals from 8 to 11.5 ha, and seasonal range sizes from 5.5 to 10.5 ha. There is no evidence for a consistent difference in range size between males and

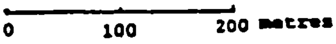
Figure 6.1 Ranges of duikers at IET from tracking data



a) Mae Mae (A♂)

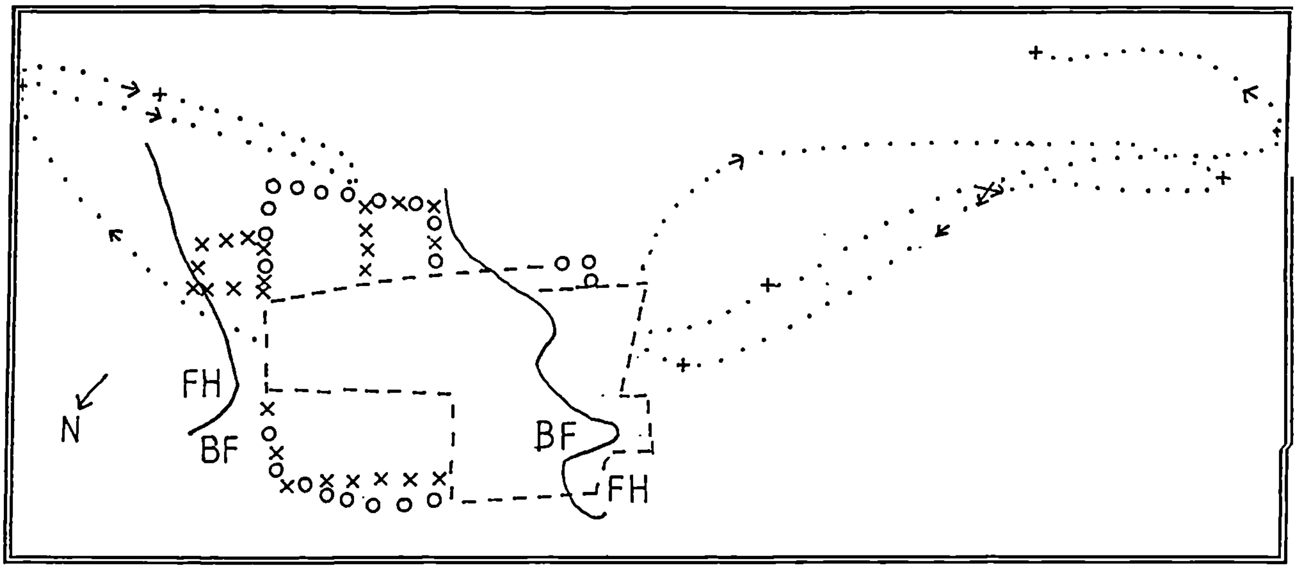


b) Christiane (A♀)

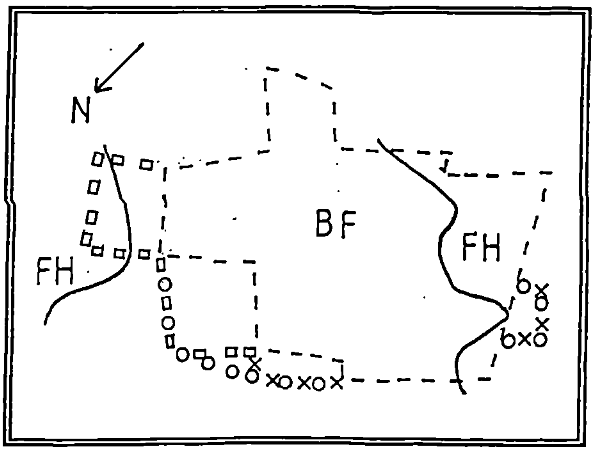


Key: - - - All seasons; ∘ ∘ ∘ December 1990 - February 1991;
□ □ □ May - July 1991; × × × September - November 1991
····· Expeditions (+ indicates sightings)
—— Habitat boundary

Figure 6.1 Ranges of duikers at IET from tracking data



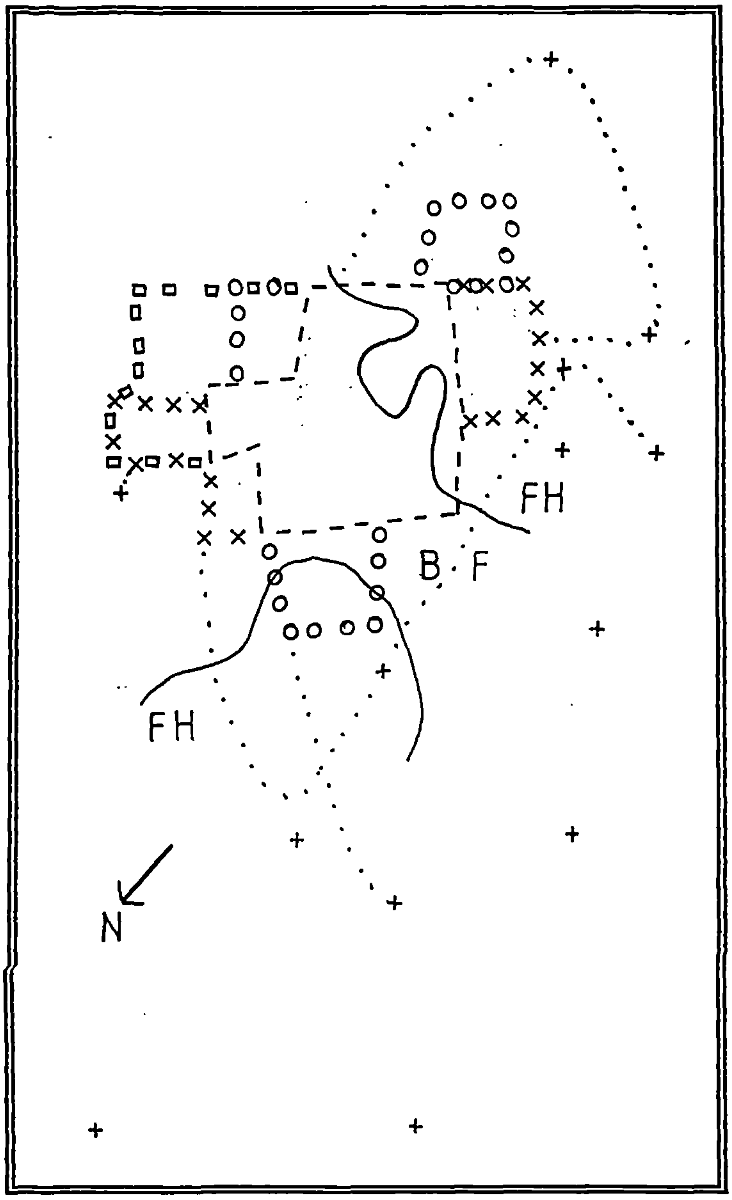
c) Lucien (A♂)



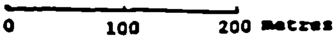
d) Germaine (A♀)

Key: - - - All seasons; ∘ ∘ ∘ December 1990 - February 1991;
□ □ □ May - July 1991; × × × September - November 1991
······ Expeditions (+ indicates sightings)
—— Habitat boundary

Figure 6.1 Ranges of duikers at IET from tracking data

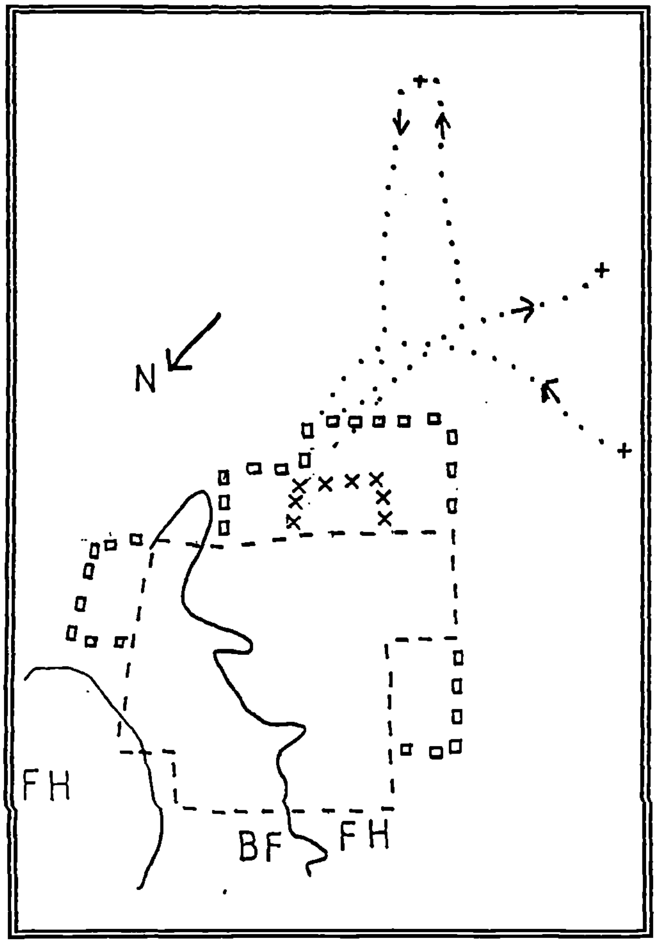


e) Gabrielle (J♀)

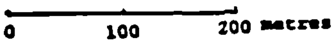


Key: - - - All seasons; December 1990 - February 1991;
□ □ □ May - July 1991; × × × September - November 1991
······ Expeditions (+ indicates sightings)
—— Habitat boundary

Figure 6.1 Ranges of duikers at IET from tracking data

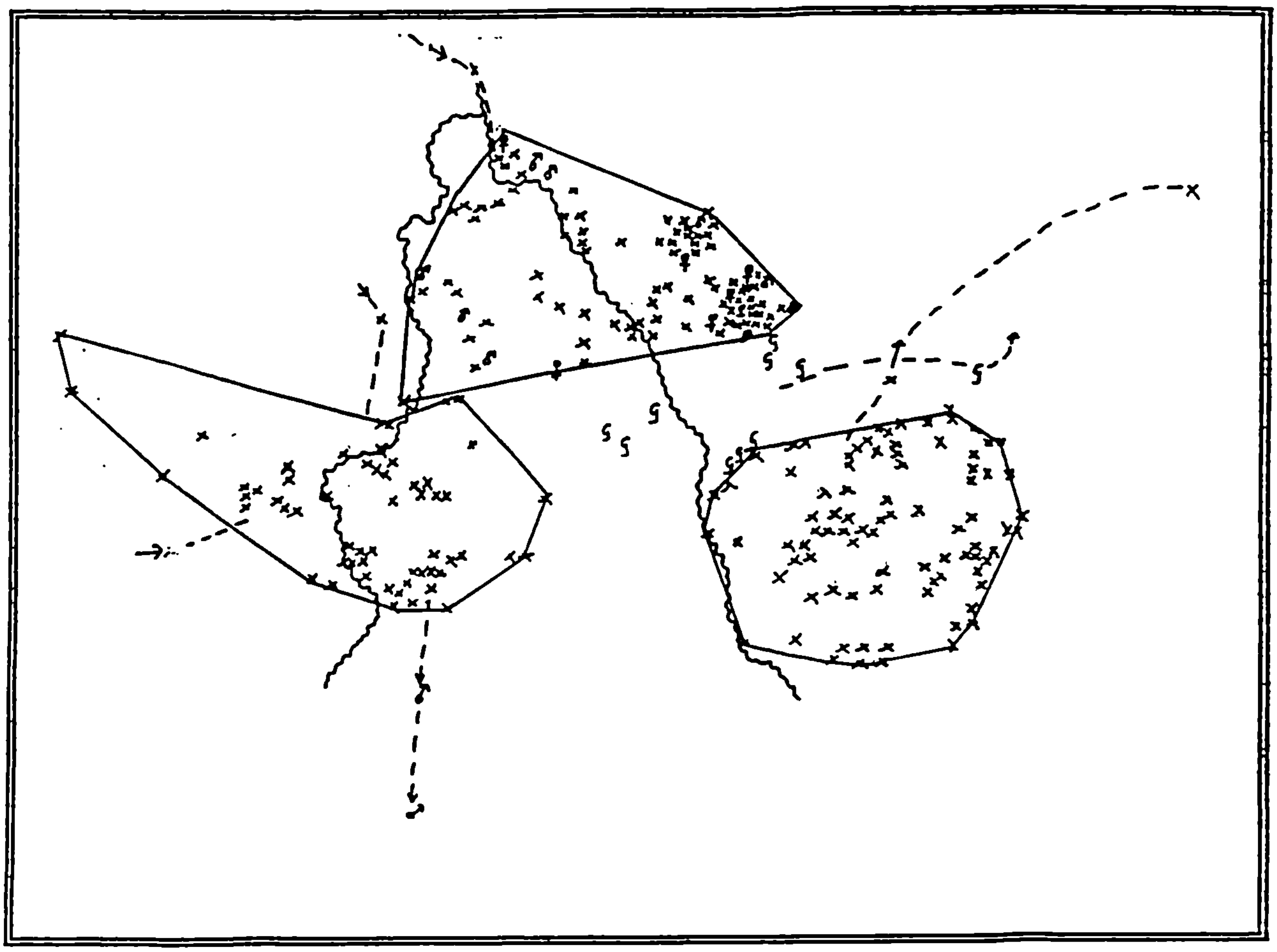


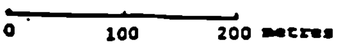
f) Lucbersone (A♂)



Key: - - - All seasons; ◦ ◦ ◦ December 1990 - February 1991;
□ □ □ May - July 1991; × × × September - November 1991
······ Expeditions (+ indicates sightings)
——— Habitat boundary

Figure 6.2
Ranges of duikers at IET from sightings





KEY

xxx Sighting

♂ Sighting of male only in pair

♀ Sighting of female only in pair

G Sighting of Gabrielle (J♀)

---+ Sighting during an expedition outside home range

~~ Stream

females, nor between seasons. From sighting data, overall range sizes for all animals were 5 to 5.5 ha.

TABLE 6.1
RANGE SIZES OF DUIKERS RADIO-COLLARED AT IET

Name	Sex & Age Class	Home Range Size (Hectares)			
		Dec-Mar	May-Jul	Sep-Nov	Total[1]
Mae Mae	A♂	6.0	7.0	10.5	11.0 (5.5)
Christiane	A♀	6.0	8.0	10.0	11.5 (5.5)
Gabrielle	J♀	5.5	5.5	5.5	8.0
Lucbersone	A♂	6.5	8.0	6.0	8.0 (5.0)
Germaine	A♀	8.0	8.5	7.5[2]	9.0 (5.5)
Lucien	A♂	9.5	7.0	7.5	10.5 (5.5)

The grid-cell analysis is likely to give an over-estimate of home range since each grid-cell represents a relatively large portion of the home range size, and whenever an animal is recorded in the edge of a new cell, the whole of that cell is added to the home range estimate. Range size estimates from sighting data were found to stabilise after about 25 data points; there were insufficient data to analyze in this way per season, but for all animals except Gabrielle there were ample data points to analyze over the whole year (n ranged from 32 to 90). Sighting locations in conjunction with tracking data suggest that there was little seasonal change in ranges (with one exception - see below); therefore it can be estimated from sighting data

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[1] Range from remote data; (range from sightings).

[2] Small sample (n=13) - killed by leopard 25/10/91.

that the true home range sizes of both male and female adult duikers are likely to be between 5 and 6 ha.

Figure 6.1 shows that two individuals, Mae Mae and Christiane, extended their range considerably towards the east in the course of the study while abandoning only a relatively small area to the west. This caused an increase in estimated range size from 6 ha in December 1990 to March 1991 to 10 ha and 10.5 ha (for Christiane and Mae Mae respectively) in September to November 1991. It is possible that the individuals occupying a neighbouring home range were killed, leaving a vacant area. For the other four duikers, cells recorded in one season only were adjacent to the central range recorded in all three seasons; thus, ranges may have extended only by some tens of metres from the central region rather than by whole cells. This is supported by the fact that for these animals, all sightings in seasonally recorded cells were within 25 metres of the cell edge nearest the year-round range, even though all sides of the cells were monitored.

6.3.1.2. Gouleako Home ranges were planned to be determined at Gouleako in the same seasons as for IET, but three of the four animals were shot by hunters before the study was complete (see below). Data are presented as far as possible for the main wet season in 1990 (September to November 1990), the main dry season (December 1990 to March 1991) and the short wet season

(May to July 1991). Ranges at Gouleako were calculated by the grid-cell method only, as there were too few sightings for analysis. They are therefore likely to be overestimates of the true range sizes, as explained above. The results are given in Table 6.2 and Figure 6.3.

TABLE 6.2
RANGE SIZES OF DUIKERS RADIO-COLLARED AT GOULEAKO

Name	Sex & Age Class	Home Range Size (Hectares)			
		Dec-Mar	May-Jul	Sep-Nov	Total
Père Abraham	A♂	6	-	5.0	7.0
Robertine	J♀	7.5	(7.5)[3]	4.0	13.0
Luis	A♂	5.0	-	-	5.0
Aline	A♀	4.5	4.0	-	6.0

Seasonal ranges vary between 4.0 and 7.5 ha, compared to 5.5 to 10.5 ha for IET by this method. Overall ranges are included for comparison with those at IET but are of limited importance since data were not completed for the whole year. They vary from 5 to 7 ha for three of the four duikers. The overall range of the juvenile female Robertine was recorded as 13 ha, due to a shift in her range. In May to July 1991 this individual was ranging widely and it was not possible to reach a plateau in the range estimate during data collection - she did not seem to be keeping within a fixed area. As a juvenile animal, she may have been leaving the

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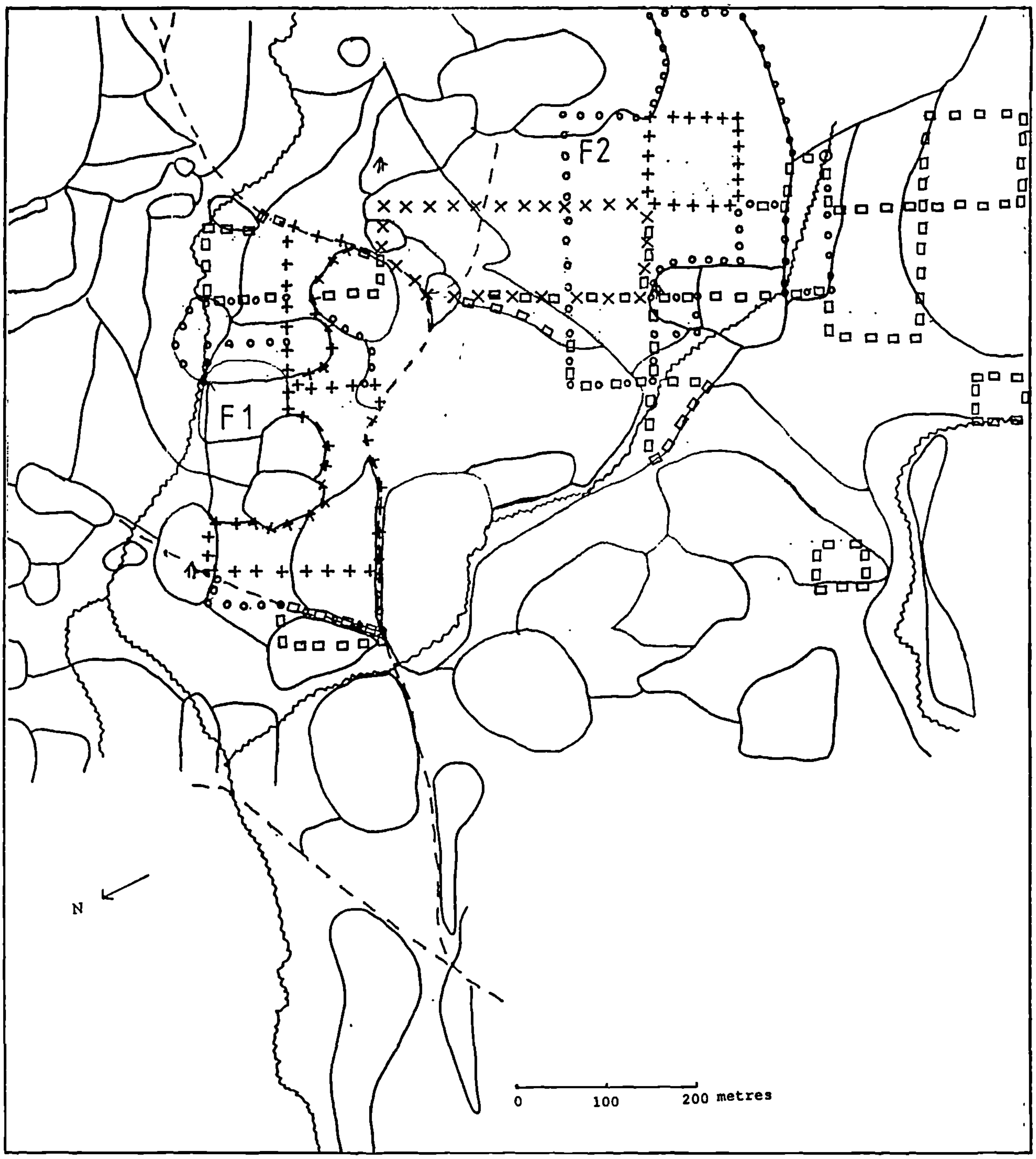
[3] Sample size insufficient - see text

Figure 6.3 Ranges of duikers at Gouleako

a) Females

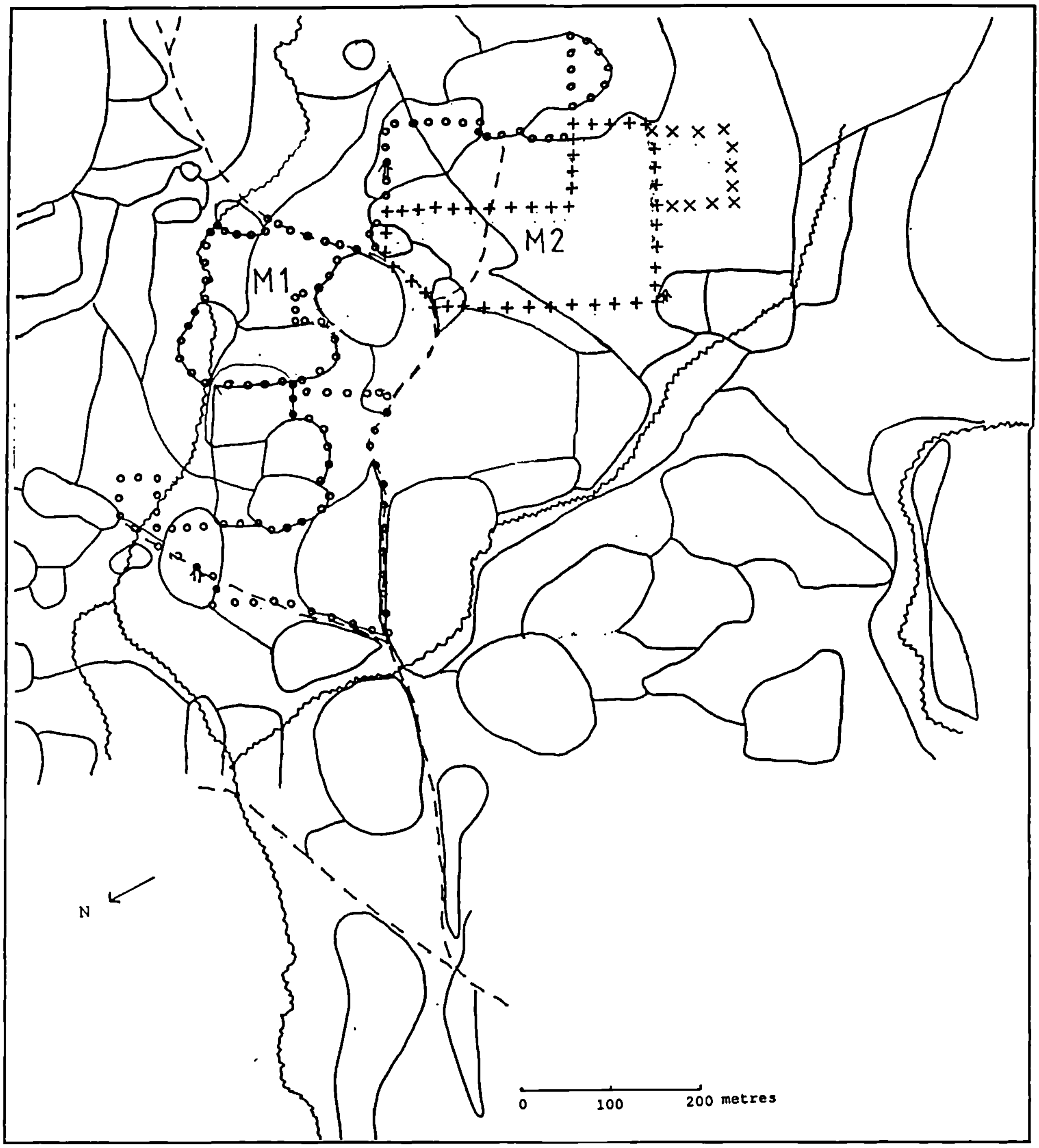


<u>Key</u>
+ + Overlap between all seasons
× × September - November 1990
∘ ∘ December 1990 - March 1991
□ □ May - July 1991
— Habitat boundaries (see Appendix 3)

F1 Aline (A♀)
F2 Robertine (J♀)

Figure 6.3 Ranges of duikers at Gouleako

b) Males



<u>Key</u> + + Overlap between all seasons
× × September - November 1990
∘ ∘ December 1990 - March 1991
▫ ▫ May - July 1991
— Habitat boundaries (see Appendix 3)

M1 Luis (A♂)
M2 Père Abraham (A♂)

parental home range to look for a mate and a range of her own; however, she was killed by hunters during this time.

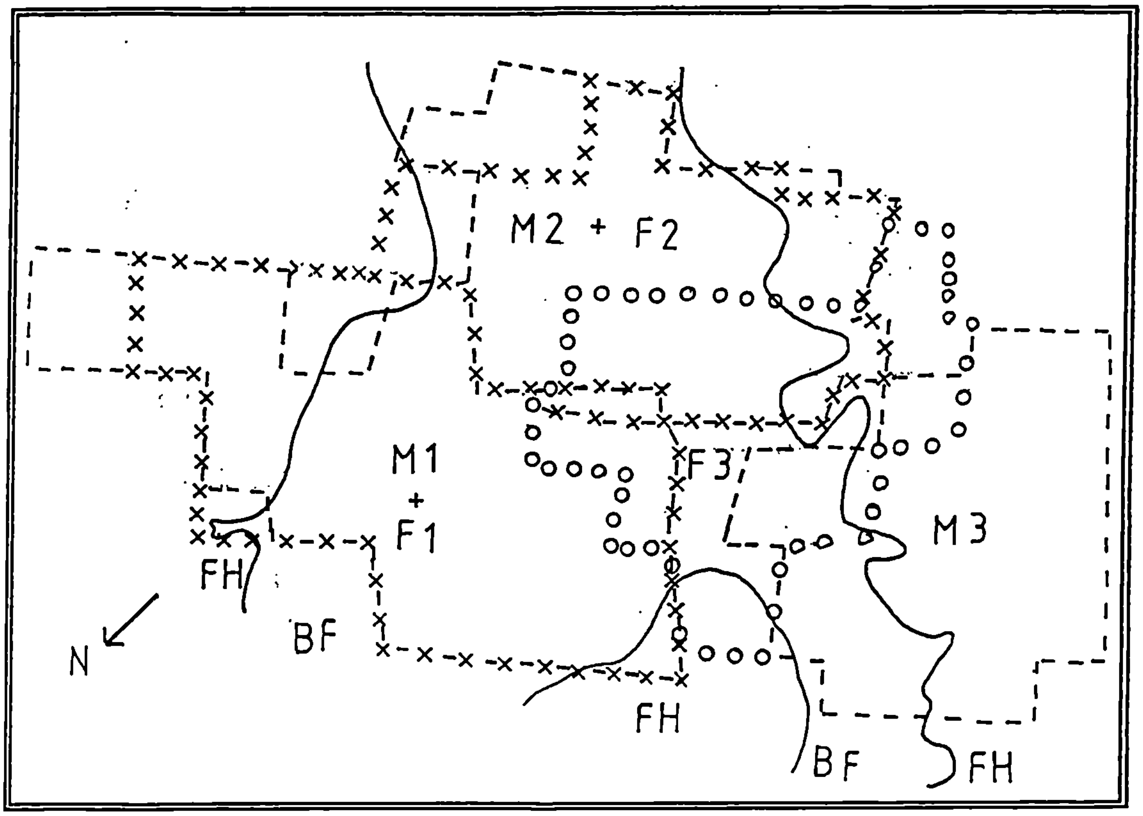
The mean seasonal home range size was calculated for adults at both IET and Gouleako. Data for Mae Mae and Christiane from September to November 1991 was omitted since they began to use a neighbouring home range. The mean at IET was 7.3 ha (range 6 to 9.5), and at Gouleako was 4.8 ha (range 4 to 5). Thus, home ranges at IET were larger than those at Gouleako. An estimate of the mean home range size at IET over the whole year, from sighting data, was 5 to 6 ha. If the proportion of overestimation by grid-cell analysis is similar at the two sites, ranges at Gouleako may be as small as 3.6 ha.

6.3.2. Home Range Overlaps

6.3.2.1. IET Summary maps of ranges determined by tracking data at IET are given for each season and for the whole study period in Fig. 6.4 which shows the overlaps between ranges.

The ranges of Mae Mae (A♂) and Christiane (A♀) overlapped by 82% (100%, 83% and 85% for the three seasons respectively); those of Lucien (A♂) and Germaine (A♀) by 80% (91% and 65% for the first two seasons; third season, incomplete data). Other overlaps between adult duikers are minimal (1% across seasons between all these four). The overlap between the range of the

Figure 6.4
Ranges of duikers at IET from tracking data, by season

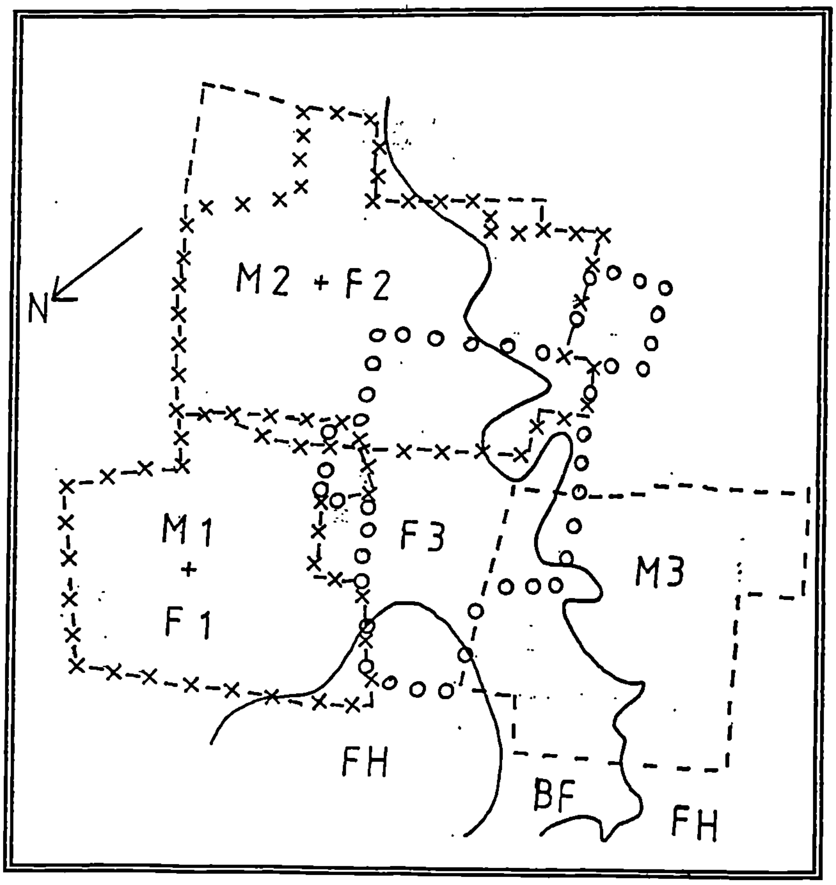


a) All seasons

0 100 200 metres

Key: - - - Adult male (M1 = Mae Mae, M2 = Lucien, M3 = Lucbersone)
x x x Adult females (F1 = Christiane, F2 = Germaine)
o o o Juvenile female (F3 = Gabrielle)
——— Habitat boundary

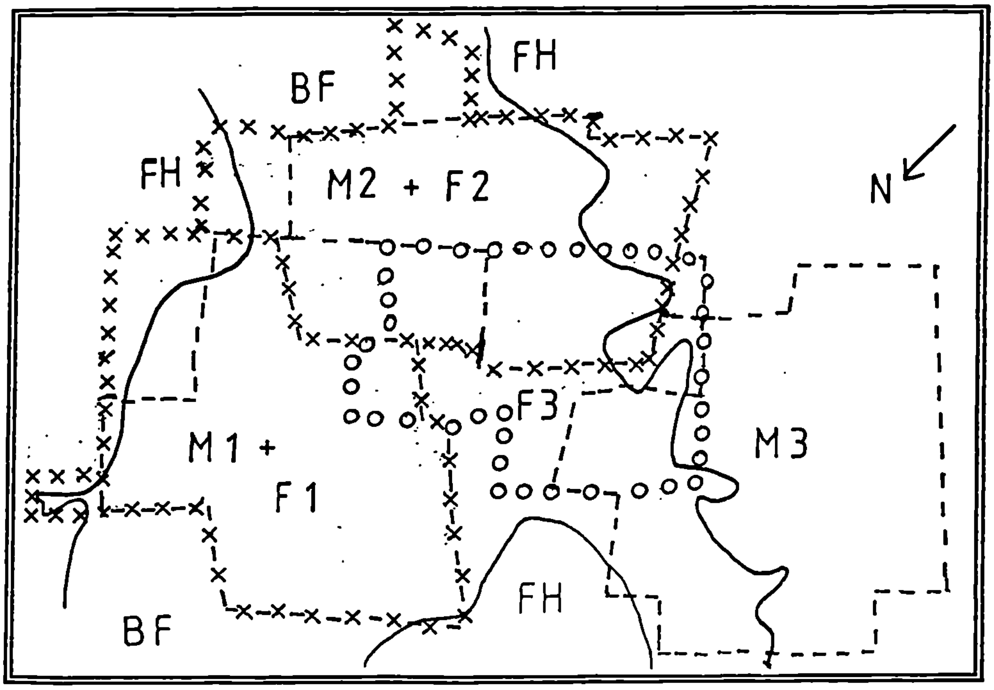
Figure 6.4
Ranges of duikers at IET from tracking data, by season



b) December 1990 - February 1991

Key: - - - Adult male (M1 = Mae Mae, M2 = Lucien, M3 = Lucbersone)
x x x Adult females (F1 = Christiane, F2 = Germaine)
o o o Juvenile female (F3 = Gabrielle)
—— Habitat boundary

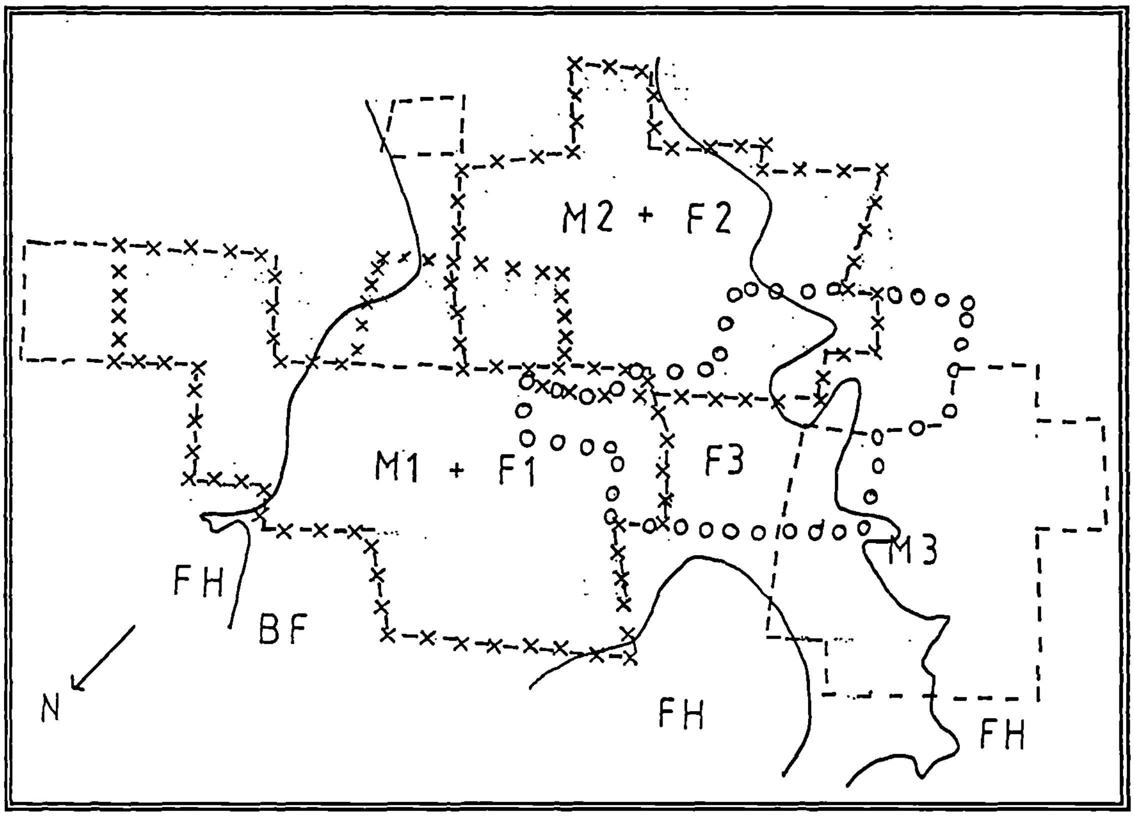
Figure 6.4
Ranges of duikers at IET from tracking data, by season



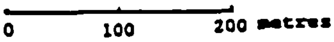
c) May - July 1991

Key: - - - Adult male (M1 = Mae Mae, M2 = Lucien, M3 = Lucbersone)
x x x Adult females (F1 = Christiane, F2 = Germaine)
o o o Juvenile female (F3 = Gabrielle)
—— Habitat boundary

Figure 6.4
Ranges of duikers at IET from tracking data, by season



d) September - November 1991



Key: - - - Adult male (M1 = Mae Mae, M2 = Lucien, M3 = Lucbersone)
x x x Adult females (F1 = Christiane, F2 = Germaine)
o o o Juvenile female (F3 = Gabrielle)
—— Habitat boundary

juvenile female Gabrielle and all others is greater - with Mae Mae and Christiane by 7% (2%, 3% and 7% for the three seasons respectively); Germaine and Lucien by 17% (13%, 17% and 9%), and Lucbersone by 10% (5%, 8% and 5%). Thus, the collared animals made up two male-female pairs, each with a joint home range; a juvenile female; and an adult male. Ranges of the two pairs and the adult male were adjacent but distinct; that of the juvenile female overlapped all three.

6.3.2.2. Gouleako Since data for Gouleako were not complete for the whole year, it was only possible to calculate overlaps between ranges for certain seasons. The December 1990 to March 1991 ranges of Luis (A♂) and Aline (A♀) overlapped by 78%. The ranges of Père Abraham (A♂) and Robertine (J♀) overlapped by 79% in September to November 1990, but by only 18% in December to March, because of a shift in the range of Robertine. There was no overlap in ranges between these two pairs. The overlaps between ranges can be seen in Figure 6.3.

6.3.3. Expeditions outside the home range

6.3.3.1. IET An expedition was defined as a trip in which a duiker travelled without stopping at least 250 m outside its normal range, spent some hours away, and travelled directly back again. This was in very clear contrast to its normal slow progress within a small, habitual area. The distance 250 m was chosen as the diameter of a typical range; thus, in an expedition, the duiker was likely to have crossed at least one neighbouring range, assuming ranges are contiguous.

Table 6.3 shows the number of days in each season that expeditions were recorded. Expeditions were recorded only for the three adult males and the juvenile female; the adult females never left their home ranges. Six of the seven expeditions by adult males were under 3.5 hours' duration and began between 0930 and 1330. The seventh started at 1000 and lasted 24 hours, involving an overnight stay about 1 km to the south of the normal range. Expeditions by the juvenile female Gabrielle were more variable, starting between 0845 and 1330 and lasting from three to six hours plus one overnight trip about 1 km northwest of the normal range.

TABLE 6.3
EXPEDITIONS OUTSIDE HOME RANGES BY DUIKERS AT IET

DUIKER	Days with expeditions/total no. days			
	Dec-Feb	May-Jul	Sep-Nov	Total
Mae Mae (A♂)	1/9	0/6	0/15	1/30 (3%)
Christiane (A♀)	0/9	0/6	0/6	0/21 (0%)
Lucien (A♂)	1/7	2/7	3/14	6/28 (21%)
Germaine (A♀)	0/7	0/7	0/5	0/19 (0%)
Lucbersone (A♂)	0/8	3/14	0/9	3/31 (10%)
Gabrielle (J♀)	1/6	3/4	1/11	5/21 (24%)

It was not possible to map expeditions accurately because of the practical difficulties of radio-tracking outside the grid-system, but approximate locations during expeditions are shown in Figure 6.1. Each of the two males who went on repeated expeditions had a preferred direction of travel; thus, Lucbersone always went south, at least as far as the next valley; Lucien also went south until mid-September 1991, when he began going east. He was twice seen returning towards his normal range from an expedition; both times he was alone and travelling fast. One expedition began one and a half hours after a prolonged chase with a neighbouring male, and took him in the direction from which the male had come. Mae Mae was only once recorded on an expedition, which began with a chase between himself and a male-female couple; later in the day he was seen repeatedly outside his range chasing the female and attempting to mount her.

6.3.3.2. Gouleako The only expedition recorded at Gouleako was by Robertine (J♀) in October 1990. She left her range at 1600 hours and travelled 500 m to the south of her range to a coffee plantation overgrown with Chromolaena odorata (Compositae). She returned the following morning at 0730 hours.

6.3.4. Habitat Use

6.3.4.1. IET Table 6.4 shows the percent of the study site and of each individual's seasonal home ranges in each of the two habitats, BF and FH.

62% of the study site was FH, and 35% BF (3% was secondary forest which fell outside the area of the radio-collared duikers). Figures for home ranges vary from 97% BF and 3% FH to 24% BF and 76% FH, showing that C. maxwelli was not restricted to either habitat.

TABLE 6.4
PERCENT AREA OF STUDY SITE AND HOME RANGES AT IET IN EACH HABITAT

	Dec - Mar		May - July		Sep - Nov	
	BF	FH	BF	FH	BF	FH
Study site	35	62	35	62	35	62
Mae Mae	96	4	97	3	68	32
Christiane	96	4	86	14	77	23
Lucien	81	19	73	27	80	20
Germaine	81	19	79	21	78	22
Lucbersone	31	69	24	76	32	68
Gabrielle	75	25	72	28	68	32

TABLE 6.5
PERCENT TIME SPENT IN EACH HABITAT BY DUIKERS AT IET

	Dec - Mar		May - July		Sep - Nov	
Individual	BF	FH	BF	FH	BF	FH
Mae Mae	100	0	95	5	92	8
Christiane	100	0	92	8	83	17
Lucien	59	41	59	41	64	36
Germaine	58	42	63	37	66	34
Lucbersone	24	76	28	72	26	74
Gabrielle	80	20	83	17	77	23

The percent of the active day spent in each habitat (shown in Table 6.5) was approximately proportional to the percent area of each habitat in the home range. There are no discernible trends in seasonal shifts in habitat use.

6.3.4.2. Gouleako Table 6.6 shows the percent of the study site and the percent of each individual's home range to fall in each habitat for each season.

The study site initially contained between 10 and 20 % each of all habitats except Chromolaena thickets (EUP) and mixed Chromolaena with young secondary thickets (EUP/JF2); by May the previous season's fields had become overgrown with Chromolaena and a few new fields had been cut, so the figures for these two habitats were reversed.

TABLE 6.6
PERCENT AREA OF STUDY SITE AND HOME RANGES AT GOULEAKO IN EACH HABITAT

Habitat	Study Site		Abraham	Robertine		Luis	Aline	
	Dec-Mar	May-June	Dec-Mar	Dec-Mar	May-June	Dec-Mar	Dec-Mar	May-June
JF2	20	20	4	2	19	20	35	40
JBF	14	14	1	11	15	8	1	10
EUP	4	18	13			17	17	32
CHA	18	4	2					
BF	10	10		1	5	12	7	
FH	19	19	61	80	51	14	8	7
VF2	13	13	19	1	6	24	27	20
EUP/JF2	3	3		5	5	5	5	1
BAM	1	1						

The home ranges of the individuals under study contained all habitats except bamboo. Fields were only recorded as 2% of Père Abraham's range in the first season, in spite of covering 18% of the study site; it can been seen from Figure 6.3 that home ranges curved around the edges of fields, showing a clear avoidance of these habitats by the duikers. Père abraham was never seen in the fields and the inclusion of this area in the home range is probably an artefact of grid-cell analysis. Heavily used man-made paths also formed a barrier; no home range crossed one (although a less well-trodden path passed through the home range of Père Abraham and Robertine). All home ranges included some areas of JF2, JBF, VF2 and FH, but the proportions varied greatly. Robertine's home range was comprised mostly of mature forest (FH), with a large percentage also of young vegetation (JBF and JF2). Père Abraham's range was also mainly FH, with a considerable area of old secondary vegetation (VF2). By contrast, Luis and Aline occupied a home range comprised primarily of secondary growth (JF2, EUP, VF2).

Table 6.7 shows the percent of the active day spent by each individual in each habitat type. There are notable discrepancies from the percentage areas given in Table 6.6. No animal was recorded in fields (CHA) and no animal spent more than 5% of the time in BF. The percent of time spent in FH was lower than the percent area of this habitat type in the home range in all cases except Aline in May to July. Père Abraham and Robertine spent a disproportionate amount of time in secondary habitats (VF2, JF2, JBF). Luis and Aline spent most of their time in _Chromolaena_ thickets from December to March; in May to June, Aline spent 56% of the time in young secondary vegetation, and less time than expected in _Chromolaena_ thickets or old secondary vegetation (VF2).

TABLE 6.7
PERCENT TIME SPENT IN EACH HABITAT BY DUIKERS AT GOULEAKO

Habitat	Abraham	Robertine		Luis	Aline	
	Dec-Mar	Dec-Mar	May-June	Dec-Mar	*Dec-Mar*	*May-* June
JF2	9	6	26	16	6	56
JBF		12	29	3		13
EUP	6			51	59	22
CHA						
BF			5	5	2	
FH	49	66	24	5	3	13
VF2	36	3	17	19	30	11
EUP/JF2		14				

6.4. Discussion

In general, it was found that a male and a female adult _C. maxwelli_ shared about 80% of their range, which overlapped only minimally (1%) with ranges of adjacent adults. There was no consistent difference in range size between the sexes. These results can be compared to those for _C. monticola_ (Dubost, 1980), which had a mean of 77% overlap between the male and female in a given territory, and a mean overlap between neighbouring females of 2% and between males of 0.2%. Again, there was no consistent difference in range size between the sexes in that species.

Ranges of adult C. maxwelli at IET were calculated as 5 to 6 hectares in size by the convex polygon method. There are no previous estimates of range size for this species, but it compares with 2.5 to 4 hectares (Dubost 1980) or 3.4 to 6.4 hectares (Hart 1984) for C. monticola, which at 4 to 5.5 kg is about half the body weight of C. maxwelli. The relationship between range size and body weight depends upon energetic needs and food availability; the former is related to basal metabolic rate (M), which is connected to body weight (W) by the equation $M = kW^{0.75}$. Harestad and Bunnel (1979) found home range size S was connected to body weight within a taxonomic and trophic group by the equation $S = kW^{1.9}$. Feer (1989) investigated the relationship for small frugivorous ruminants and modified the equation to $S = 5.13\text{x}10^{-7}\text{x}W^{1.82}$, based on data for females of three species of Cephalophus and Hyemoschus aquaticus. Taking the body weight of C. maxwelli as 10 kg, by this model it should have a home range size of about 9.8 hectares, but the range sizes found were only about 5 to 6 hectares. The discrepancy may be connected to differences in food availability between the two sites, or to a difference in food choice or foraging strategies between C. maxwelli and the other species above.

Ranges were smaller at Gouleako than at IET, even though edible fruits were less abundant (Chapter 5).

Territories of adults were almost constant throughout the study - only one couple showed a significant range shift, when their range was expanded to the east. One hypothesis for the expansion is that a neighbouring home range was vacant following the death or emigration of its occupants. Latrines at IET were found to be stable over at least two years (see chapter 7), suggesting that territorial boundaries are also stable. Home ranges at Gouleako are likely to change more frequently because of rapid changes in habitat distribution as young vegetation matures.

Ranges of the two juvenile females tracked showed some discrepancies from the characteristics of adult ranges. One juvenile at Gouleako shifted her range by at least 70% between each of the three seasons recorded, and in the last season (May to July 1991) did not stay within a defined territory but ranged widely. The juvenile female at IET spent most of her time within a fixed area throughout the study, although on 24% of days on which she was tracked, she left this area for part or all of the day; in some cases she travelled over a kilometre away and stayed away overnight. Unlike the territories of adults, her range overlapped considerably with all three neighbouring groups which were studied (by 7%, 17% and 10%). These were the only two females to be recorded outside fixed territories, and it is likely that they were at an age to emigrate from the parental territory. At the end of the study when the (then) subadult female at IET was caught, she was accompanied by an adult male and was in the last stages of pregnancy; unfortunately she was extremely wary of observation and it is not known whether the male was habitually with her in her home range.

Expeditions away from the territory were recorded for all three males at IET, but neither of the two males at Gouleako. Interestingly, Dubost (1980) mentions expeditions away from the territory by male C. monticola; the male would travel 100 to 300 m outside his territory to spend a few hours feeding on a fruit-patch. In addition, when a female was about to give birth, the male would leave the territory and live alone or with another female, coming back for only about 25% of his time. However, the expeditions by C. maxwelli do not correspond to either of these cases; they were not seasonal, so could not be linked to births, and no fruit-patches were found which could explain the trips. Dubost reports that during expeditions, the male would travel quickly and nervously to a fruit-patch, eat concentratedly and return directly to his own territory. By contrast, the male C. maxwelli in this study spent almost the entire time of the expedition travelling and usually followed a long, circular route rather than going directly there and back. In two of the ten recorded expeditions by males, the trip started with a dispute with a neighbouring male, in one case in the presence of a neighbouring female which the collared male repeatedly tried to mount. It seems therefore that these expeditions are connected with sexual and territorial activity rather than feeding; they may be triggered by an encounter with a neighbouring male or receptive female at a territorial border.

Analysis of data in Chapter 5 showed that edible fruits were more abundant at IET than at Gouleako; at IET they were most abundant in FH, and at Gouleako in primary rather than secondary vegetation. If home range size were determined primarily by food availability, home ranges should be larger at Gouleako than at IET; but the reverse was true. No increase in home range size was found in the season of fruit scarcity (May to July). Similarly, no preference was found at IET for FH over BF, although the one home range recorded as primarily on FH may have supported three adult animals, in contrast to two for all other home ranges (see Chapter 7). Data on habitat preferences at Gouleako showed that individuals used a mix of primary and secondary habitats, and in fact spent more time in secondary habitats than expected from the area make-up of the ranges. In particular, two individuals spent over half their time in *Chromolaena* thickets, even though *Chromolaena odorata* is highly toxic and had the lowest density of edible fruits. Open areas such as fields and major man-made paths were avoided. Thus, fruit availability did not appear to be the main factor determining home range size or habitat preferences.

The greater risk from hunting at Gouleako was dramatically demonstrated by the killing of three of the four animals at Gouleako by villagers during the study, compared with the death of one animal of six at IET, which was killed by a leopard. It is likely that the risk from hunting was the primary factor determining habitat preferences at Gouleako, and may have been responsible for reduced mobility and smaller home ranges.

CHAPTER 7. BEHAVIOUR OF Cephalophus maxwelli

7.1. Introduction

This chapter deals with three aspects of behaviour: daily activity cycles, social behaviour and behaviour of infants.

Activity patterns were studied by remote censusing of radio signals throughout the day and night, with the primary aim of determining whether C. maxwelli is diurnal, nocturnal or active around the clock. In addition, a brief pilot study at Monrovia zoo from December 1989 to January 1990 gave an indication of activity patterns of other duiker species found at Taï, plus the bushbuck (Tragelaphus scriptus) and the water chevrotain (Hyemoschus aquaticus).

C. maxwelli's closest relative, C. monticola, is exclusively diurnal, with activity peaks at either end of the day (Dubost, 1980; Crawford, 1984; Hart, 1984). However, limited reports on C. maxwelli in the wild suggest it to be crepuscular or nocturnal (Baudenon, 1958), whilst captive studies have concluded that it is active both night and day (Aeschlimann, 1963). The findings of the present study on activity patterns are presented in Section 7.2.

C. monticola live in monogamous family groups with one or two offspring (Dubost, 1980); each individual defends the group's territory against conspecifics of the same sex. Defence is by marking with urine, dung and gland secretions throughout the territory, and also by horning the vegetation. Previous reports of C. maxwelli in the wild suggest that they live solitarily or in pairs (Baudenon, 1958). However, in captivity it has been found that one male can be kept with two females and offspring. Adult males would fight violently if housed together, but young females were tolerated in their natal group into adulthood and one was mated by the father although its mother was still present. Unknown adult females were chased repeatedly by resident females. Both males and females in captivity showed territorial behaviour such as the repeated use of marking features (dung-piles, scent-marking posts, horned plants) and antagonism to conspecifics in neighbouring enclosures (Aeschlimann, 1963; Ralls, 1974, 1975).

Social behaviour and infant behaviour were studied primarily by direct observations. Data on social behaviour are presented in section 7.3, including group size and structure, together with occasional observations of interactions between animals. Additional information on territorial marking was gained by studying the distribution of latrine areas.

Section 7.4 gives a largely anecdotal account of the behaviour of infant C. maxwelli, based on opportunistic observations and regular watches of one infant in a radio-tracked group.

7.2. Activity Patterns

7.2.1. Methods In order to determine daily activity patterns, each duiker was recorded throughout the day as either active or resting. Changes in the speed of the signal (caused by the mercury tilt-switch) and also irregular changes in volume (often caused by changes in orientation of the transmitting antenna or changes in location) were taken to indicate activity. The duiker was recorded as resting only if the signal stayed constant for a full minute. Initially, activity data were collected at 30-minute intervals day and night. Once it was established that the duikers were diurnal, I attempted to balance data samples for two-hour periods between 0630 and 1830 hours. This was not always possible because varying weather conditions and spacing of the duikers affected the number of duikers within radio range. In the analysis, therefore, a subsample was taken of 30 records for each duiker in each two-hour period.

At Monrovia zoo, animals were observed at hourly intervals and recorded as active or resting. The mean percent of the time they were active was calculated for each species during the night (1830 to 0600) and the day (0630 - 1800).

7.2.2. Results Initial data collection showed that Maxwell's duikers were principally diurnal at both study sites. Between 1900 hours and 0530 hours only 14% of readings at IET (n = 79) and 19% at Gouleako (n = 393) showed that animals were active. It was not possible to approach active duikers at night without causing disturbance unless they were near a transect, and once it was established that they were principally diurnal, data collection at night was discontinued. However, night sightings of duikers throughout the study period confirmed that they remained predominantly inactive at night. Most animals seen at night were lying down when first encountered, and occasionally an animal was seen lying in exactly the same place twice in a night, with an interval of some hours between the two sightings. When an animal was found by radio both at dusk and at dawn the following day, it was always in the same grid-cell (n = 29). I gained a strong impression that the duikers moved at night only when disturbed and settled down again within a few minutes.

The duikers became active between 0600 and 0630, and went to rest between 1830 and 1900, making an active day of 12 to 13 hours. In order to look at activity patterns during the day-time, the subsample taken for each animal in each 2-hour period of the day was balanced for 30-minute sub-intervals, and as far as possible for seasons (this was not entirely possible because of deaths of animals in the course of the study, and therefore no analysis of seasonal variation is offered). One adult male (Luis) was killed within 2 months of capture, and as a result only 16 records are available for each 2-hour period.

Mean activity rates are shown for males (n = 5) and females (n = 5) in Figure 7.1, and for IET (n = 6) and Gouleako (n = 4) in Figure 7.2.

Figure 7.1 Mean daytime activity rates for male and female Maxwell's duikers

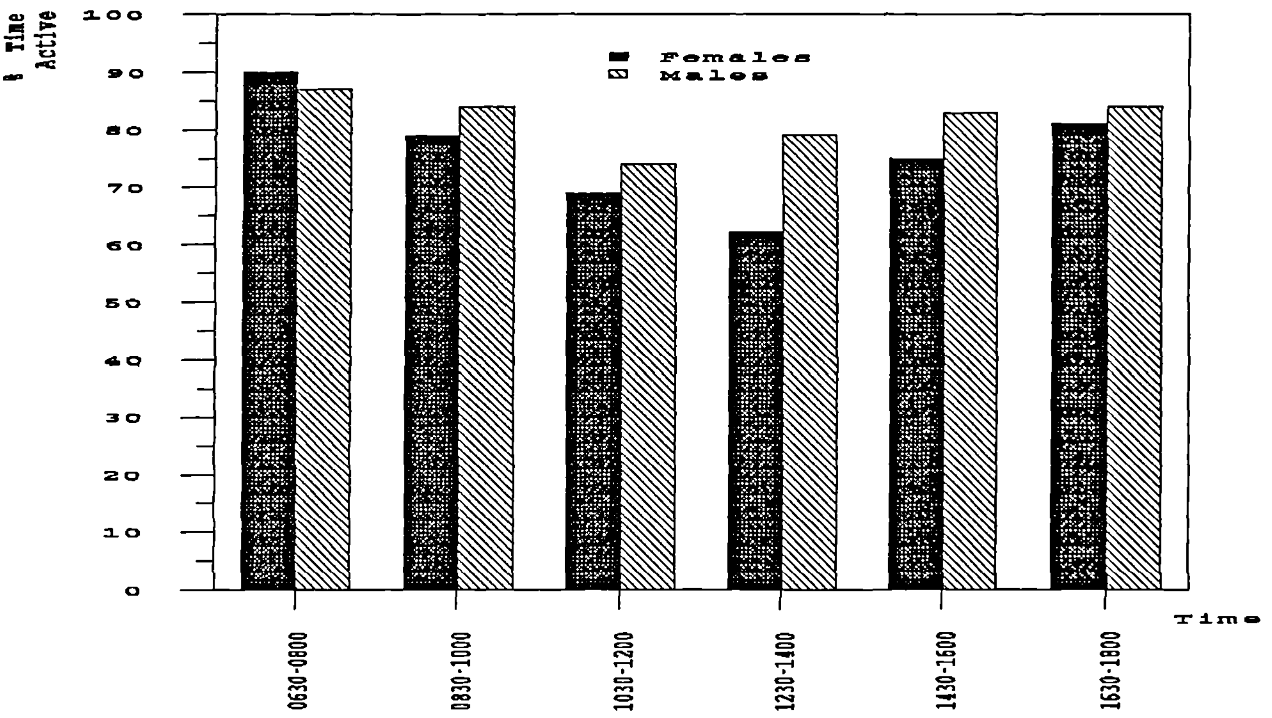
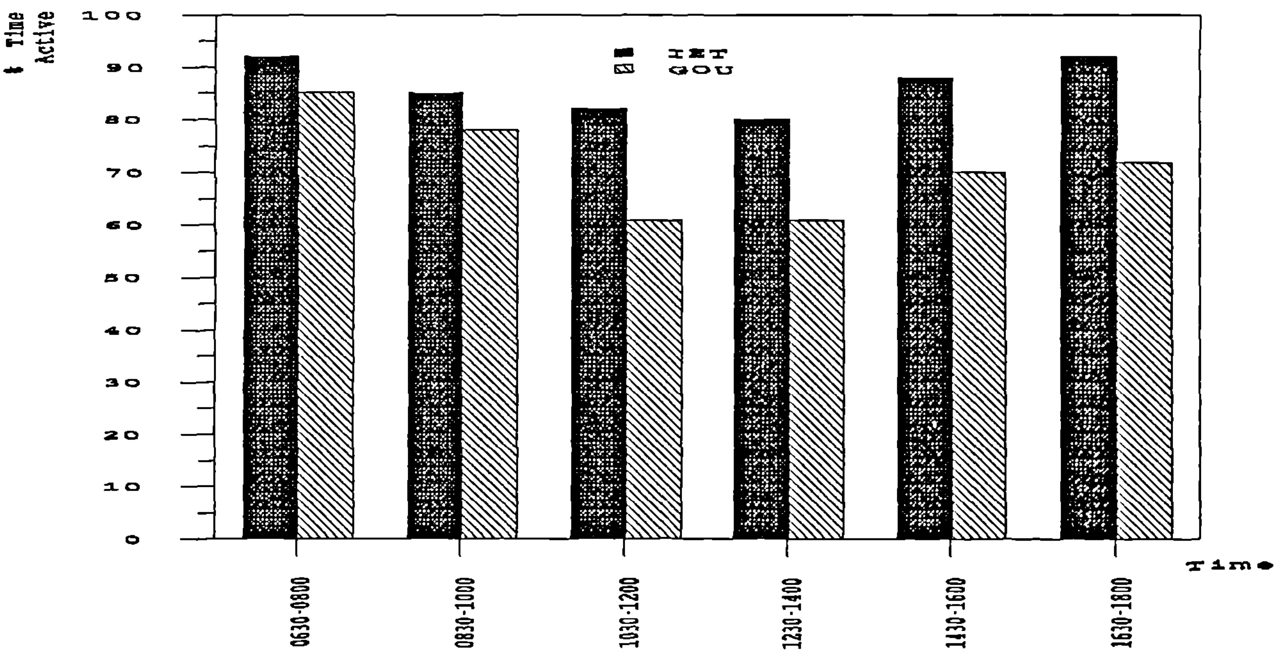


Figure 7.2 Mean daytime activity rates for Maxwell's duiker at IET and Gouleako



Activity is highest just after dawn (between 0630 and 0800) and in the late afternoon (between 1630 and 1800). It is lowest in the middle of the day, from 1030 to 1400, but even at this time duikers were recorded as active in over 60% of cases.

At IET, all three females were slightly less active than the three males (ranging from 83% to 86% and 88% to 90% of time spent active respectively). At Gouleako, the two females were active 63% and 71% of the time, and the two males 78% and 70% of the time. The less active male was Luis, for whom the sample size is small. The number of animals is too small to test statistically for individual differences, but the data suggest that males were more active than females during the day-time.

A difference in activity levels is also discernible between the two study sites. The four animals at Gouleako spent more of the day-time resting than the six at IET (22-37% at Gouleako compared with 10-17% at IET). Figure 7.2 shows that this difference is apparent at all times of day, with the greatest difference in the middle of the day between 1030 and 1400.

The results of the study at Monrovia zoo are given in Table 7.1. Animals were classified as diurnal or nocturnal if they spent over twice as much time active in one period than the other. The results suggest that the four smallest species of duiker are diurnal, C. dorsalis and Hyemoschus aquaticus are nocturnal, and C. jentinki, C. sylvicultor and T. scriptus are active both day and night.

Table 7.1 Mean Percent time active during the night and day for duikers, bushbuck and water chevrotain at Monrovia zoo

Species (number of individuals in brackets)	Mean % of time active		Nocturnal or diurnal
	Day	Night	
C. maxwelli (2)	64	21	D
C. zebra (2)	71	7	D
C. niger (5)	69	24	D
C. ogilbyi (1 juvenile)	58	17	D
C. dorsalis (14)	17	65	N
C. jentinki (1)	28	40	D+N
C. sylvicultor (6)	39	26	D+N
Tragelaphus scriptus (4)	61	47	D+N
Hyemoschus aquaticus (1)	4	67	N

7.2.3. Discussion Dubost (1980) describes a general rule connecting body size and diet with activity patterns for frugivores and folivores. He shows that small frugivores are usually either diurnal or nocturnal (Agouti paca, C. dorsalis, C. monticola, Dasyprocta punctata, Hyemoschus aquaticus), whilst frugivores with a body weight greater than 22 kg (such as C. sylvicultor) and small or large folivores (Hydrochoerus hydrochaeris, Neotragus batesi, Tapirus terrestris) are mostly active during both day and night. He suggests that small frugivores are able to satisfy their dietary needs in a shorter active day because small fruits are abundant in the forest, whereas large frugivores which eat large, dispersed fruits must spend more time collecting their food. Folivores can quickly eat a large mass of food, but since leaves are nutritionally much poorer than fruits, they need more bulk than a frugivore of comparable size. Thus, folivores and large frugivores may not be able to afford to spend the day or night resting. Based on Aeschlimann's study (1963), Dubost cites *C. maxwelli* as active night and day, and thus an exception to the above pattern. However, this species is active predominantly during the day-time and thus fits the general pattern. The results from Monrovia zoo also fit the pattern; *Hyemoschus aquaticus* and the five smaller duikers are all small frugivores and are either diurnal or nocturnal, whereas the three large species are all active both day and night. The low level of night-time activity found in *C. maxwelli* in the wild may be similar to that found in *C. monticola*, consisting of licking, stretching and changing rest-place (Dubost 1980). At Monrovia zoo, nocturnal animals awoke during the day during the two feeding-times, and some species classified as diurnal were active for up to 24% of the time at night. These relatively high figures may be due in part to artificial lighting at night, and to the effect of repeated visits by the author.

At Taï during the day-time, *C. maxwelli* showed a bimodal pattern of activity with peaks after dawn and in the late afternoon. Aeschlimann (1963) and Baudenon (1958) also reported dawn and late afternoon activity peaks for this species. Among other duikers, Dubost (1980) reported activity peaks for C. monticola from 0600 - 0900 hours and from 1500 - 1900 hours. He found a slight seasonal variation; the peaks were less acute in the dry season, when sometimes there was an extra burst of activity in the middle of the day. This was when food was most scarce, and it is possible that extra activity was necessary for foraging. Feer (1988) reported that C. callipygus showed a clear bimodal activity pattern for some individuals, and a less clear slowing of activity in the middle of the day for others.

A bimodal activity pattern is common in a wide range of animals of all taxonomic groups. To some extent, especially in the tropics, it reflects the daily temperature pattern, as animals tend to rest in the midday heat. However it can also occur for nocturnal animals (C. dorsalis, Feer, 1988, 1989; Hyemoschus aquaticus, Dubost, 1975). Some nocturnal activity peaks, especially in the early hours of the morning, may coincide with the coldest part of the night.

Male C. maxwelli were found to be significantly more active than females. Both Dubost (1975, H. aquaticus) and Feer (1988, C. callipygus and C. dorsalis) have reported the reverse for their study species, and Dubost has suggested that since females are larger than males in these species, and are usually gestating or lactating, their metabolic needs are greater and cause a noticeable increase in foraging time. However, Feer reports that although free-living male C.

dorsalis spent less time active than females, they spent more than twice as much time as females on locomotory activity, which may be related to sexual or territorial behaviour. In captivity, males spent more time active than females, perhaps because when artificially fed, females did not need extra time to forage, whereas males still spent more time on sexual or territorial behaviour. For C. maxwelli, it is possible that in Taï, food is sufficiently abundant that females need little (if any) extra time foraging, and any such difference between the sexes is offset by the extra time spent on locomotory activities by males. Further direct observations of activity are needed to test this by determining time budgets for males and females.

Activity of C. maxwelli was greater in the forest at IET than at Gouleako. Duikers at Gouleako may minimise activity in order to avoid disturbance by villagers, who hunt in this area. It has already been shown that duikers at Gouleako spend more time than expected in thick secondary growth and avoid open habitats, which also suggests avoidance of disturbance (Chapter 6).

7.3. Social behaviour

7.3.1. Methods Social behaviour was studied from direct sightings of Maxwell's duikers - both opportunistic sightings, and more intensive observations of radio-collared individuals. The methodology is outlined in Section 2.6.

The following data relevant to social behaviour were collected for each clear sighting:

Group size
Group composition
Group leadership and spacing during travel
Intragroup interactions
Intergroup interactions

These will be dealt with in turn in Sections 7.3.2.1 - 7.3.2.5.

Additional information was gathered on territorial marking by determining the distribution of latrines in relation to the ranges of radio-collared animals (for methodology, see Section 2.7). The results are presented in Section 7.3.2.6 and are compared with the ranges determined in Chapter 6.

7.3.2. Results

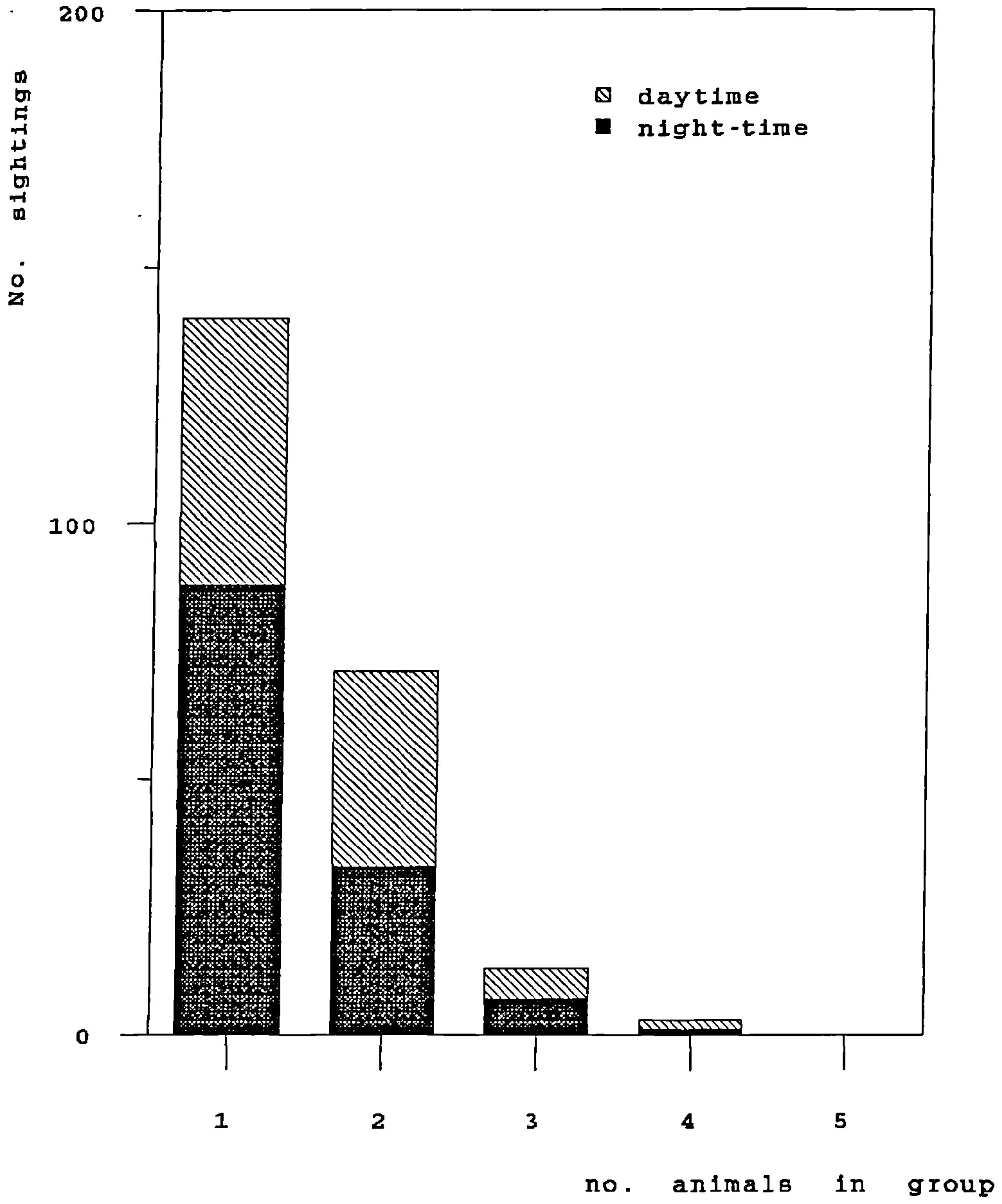
7.3.2.1. Group size Although a χ^2 test showed no difference in distribution of group sizes for opportunistic day-time sightings (n = 98) and for sightings made during radio-tracking (n = 281) (χ^2 = 4.91, 3 d.f.'s, n.s.), group sizes differed between radio-tracked groups. Therefore, mean group size was determined from opportunistic sightings alone (n = 98). Group sizes recorded from opportunistic sightings of duikers by night and by day at IET are shown in Figure 7.3.

52 (53%) of day-time opportunistic sightings were of single animals, 38 (39%) of pairs, 6 (6%) of threes and 2 (2%) of four animals. The mean group size was 1.57 and the maximum group size recorded was four, although five were seen together twice during observations of radio-tracked groups. There was no obvious seasonal variation in group size, and sample sizes were too small to test statistically. For night-time sightings at IET, 81 (69%) of 118 sightings were of single animals and the mean group size was 1.39. There was no evidence for seasonal variation in group size at night (χ^2 = 2.04, 3 d.f.'s, n.s.). The difference in group size by day and by night was significant (χ^2 = 13.49, 3 d.f.'s, $p<0.05$); animals were more often seen alone by night than during the day, even though animals were more likely to be overlooked by day owing to their escape behaviour.

During day-time capture drives at IET, five single animals were seen, and three couples.

Sightings of groups at IET containing radio-collared animals confirmed that each of the two pairs collared, plus young, made up a complete group. The third male, Lucbersone, shared his range with two adult females, who however repeatedly evaded capture. It is not known to what degree their ranges overlapped, but they were both seen in all parts of the male's range and were seen together on a number of occasions. In 1991, two

Figure 7.3 - Group sizes from opportunistic sightings



juveniles were present in the group, and on two occasions all five animals were seen resting together and intergrooming. Thus it is shown that Maxwell's duikers live in monogamous or occasionally polygynous groups.

Radio-tracking data from groups where both an adult male and an adult female were tagged were analyzed to see how much time the two animals spent in the same grid-cell. Mae Mae (♂) and Christiane (♀) were recorded in the same block in 86% of cases (n = 134); Germaine (♀) and Lucien (♂) in 56% of cases (n = 80), and Aline (♀) and Luis (♂) at Gouleako in 75% of cases (n = 44). The results for each season are shown in Table 7.2. For the two pairs for which data are complete, most time was spent together from December to March.

TABLE 7.2
TIME SPENT BY RADIO-TAGGED MALE AND FEMALE OF THE SAME GROUP IN THE SAME GRID-CELL

	Mae Mae + Christiane		Germaine + Lucien		Aline + Luis	
	T[1]	A[1]	T	A	T	A
Dec 90- Mar 91	43 (96%)	2 (4%)	31 (89%)	4 (11%)	33 (75%)	11 (25%)
May - Jul 91	18 (82%)	4 (18%)	5 (23%)	17 (77%)	no data (Luis dead)	
Sep - Nov 91	54 (81%)	13 (19%)	9 (39%)	14 (61%)	no data (Luis dead)	
TOTAL	115 (86%)	19 (14%)	45 (56%)	35 (44%)	33 (75%)	11 (25%)

[1] T = Together, A = Apart

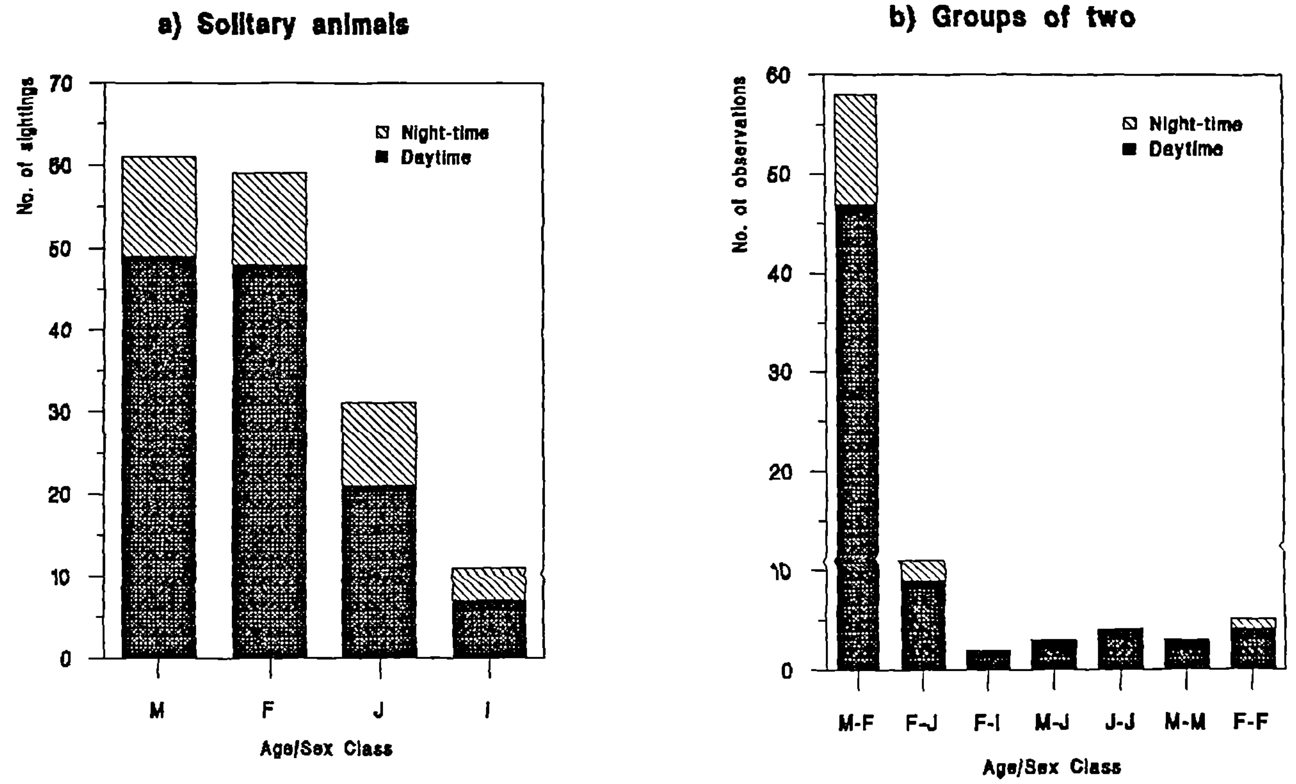
At Gouleako, only 17 opportunistic observations of Maxwells' duikers were made, and due to the poor visibility it was felt that group sizes recorded were not reliable. During capture drives in Gouleako, five couples and one single animal were recorded. During radio-tracking, three pairs and one single animal were seen.

7.3.2.2. Group composition Age and sex structure of singles, pairs and groups of three or more animals are shown in Figure 7.4 for all observations where the age and sex of animals was known. Both opportunistic observations and those from radio-tracking were used.

Singles: There was no significant difference in the proportion of males, females and young seen by night or by day (χ^2 = 3.56, 2 d.f.'s), so the two sets of data were combined (n = 162). Approximately equal numbers of adult males (38%) and females (36%) were seen.

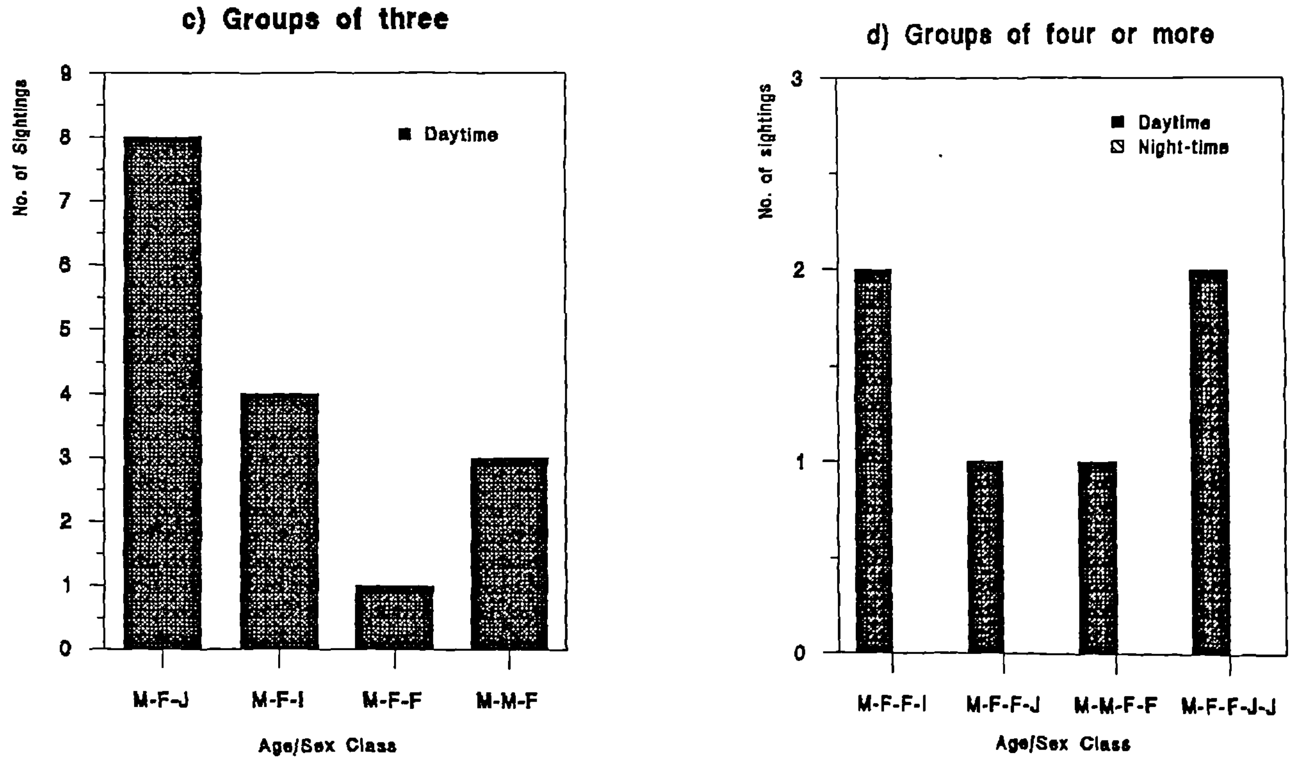
Pairs: Again, there was no significant difference between night and day-time data (χ^2 = 1.33, 2 d.f.'s), so they were analyzed together (n = 86). 67% of pairs of animals identified to age and sex were male-female pairs, and a further 16% were female-infant or female-juvenile pairs. More rarely, pairs consisted of an adult male and a juvenile, two juveniles, two adult males or two adult females.

Figure 7.4 Numbers of sightings of groups of Maxwell's duikers by age and sex structure



a) Solitary animals

b) Groups of two



c) Groups of three

d) Groups of four or more

Groups of three or more: For groups of three, age and sex of group members was determined in only 16 cases. For 12 of these, the group consisted of an adult male, adult female and an infant or juvenile; for the remaining four, of either an adult male with two females (once) or two adult males and one female (three times - once during a chase and twice when the male Lucien was following a neighbouring group, after Germaine was killed). Groups of four or five consisted of one adult male with two females and young, except for one case of a group of two adult males and two adult females, again when Lucien was following a neighbouring group.

Overall: Taking all group sightings together, it is possible to work out the overall proportion of different age and sex categories. Of 412 individuals, 154 (37%) were adult males, 173 (42%) were adult females, 66 (16%) were juveniles and the remaining 19 (6%) were infants. Thus, there were slightly more females than males. The number of infants seen is likely to be artificially low, since until about three months of age they spend much time motionless and hidden.

7.3.2.3. Group leadership and spacing during travel

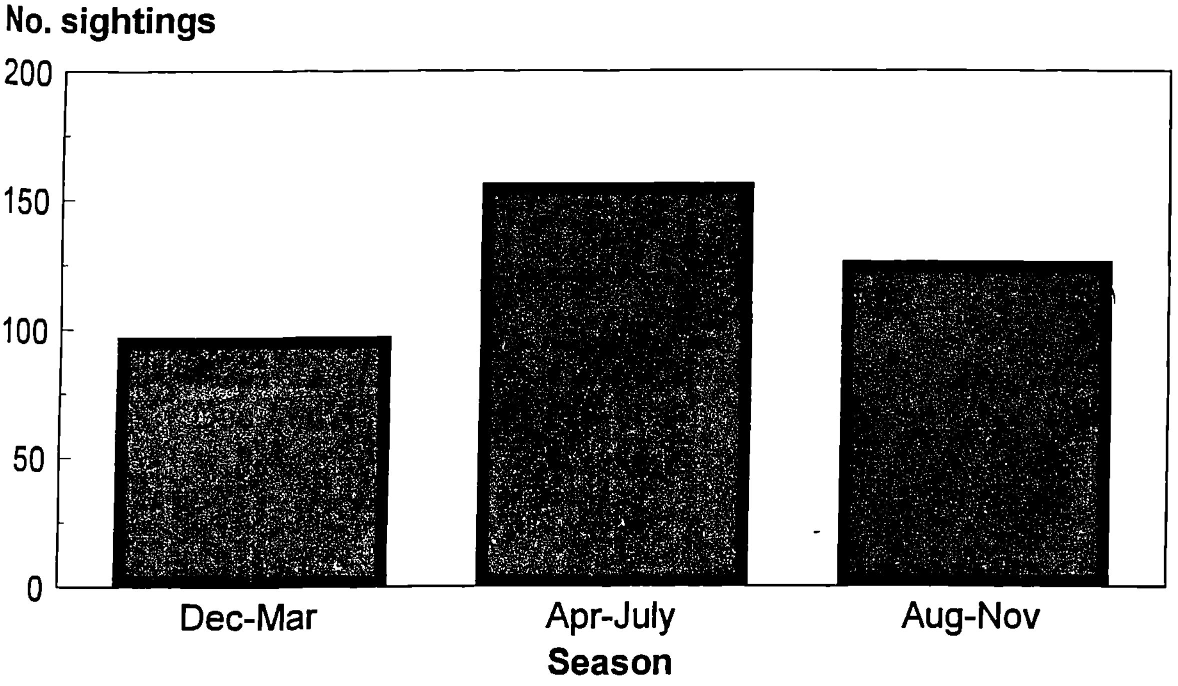
In 52 records from the groups with radio-collared animals, the adult female led the group 33 times, the adult male 13 times, and infants or juveniles 6 times. Inter-animal distances were not generally recorded, but adults were seen travelling as close together as 2 metres, and also following each other after up to three minutes' delay along well-worn paths. Females and infants often travelled almost within physical contact when together, but infants were also seen travelling alone (see section 7.4 on infant behaviour, below).

7.3.2.4. Intragroup interactions Observations of overt social interactions were rare, even when radio-collared groups were observed for extended periods (up to 30 minutes). Grooming between adults was seen only three times - once between a male and a female, once between two females, and once between two males. Females were observed grooming juveniles twice, and a juvenile was seen grooming another juvenile once.

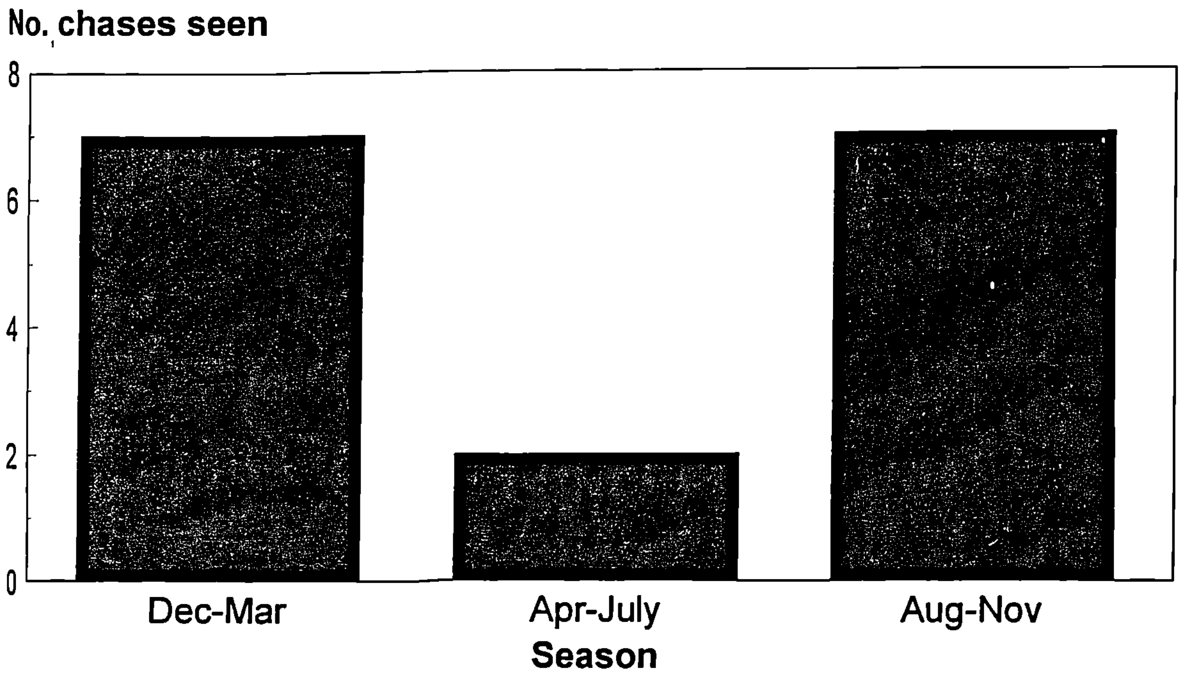
7.3.2.5. Intergroup interactions Individuals of neighbouring groups occasionally chased each other through the forest at high speed. Figure 7.5 shows the number of chases seen in each 4-month period, together with the total number of day-time sightings of duikers where group size was determined. Eighteen chases were observed. The sample is too small to test for seasonality, but there were fewer chases from April to July even though this was the period with most sightings. In all cases, the chaser was a male. In six cases he was chasing another male, in seven cases a female, and in five cases a male-female pair. The chases were often overtly aggressive; twice, a male being chased was actually bowled over by the chaser. On two other occasions, extended chasing was interrupted by

Figure 7.5 Total numbers of sightings and numbers of chases seen in each four-month period

a) Total numbers of sightings of duikers



b) Numbers of chases seen

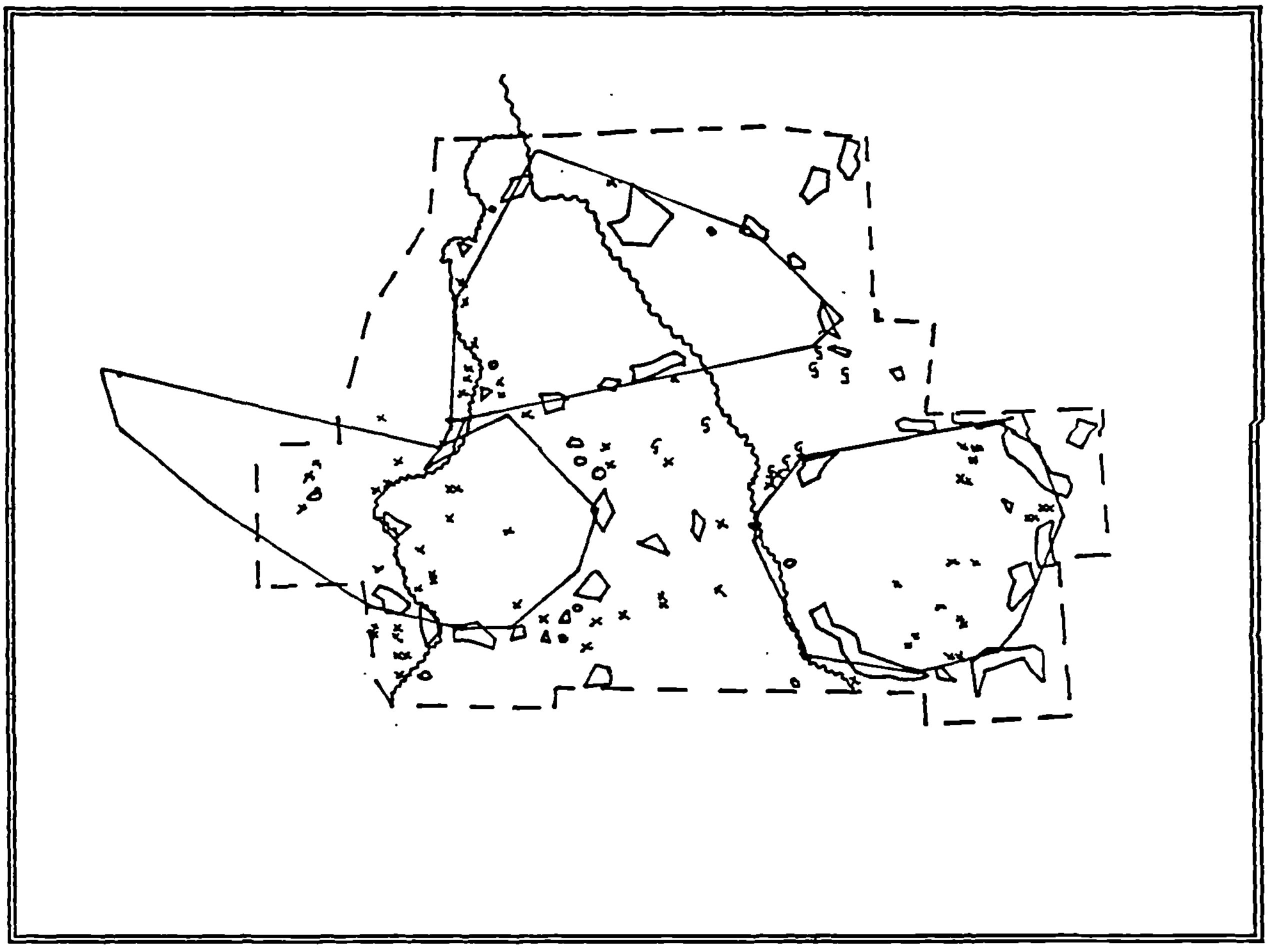


quick bouts of display by the chaser, in which he pawed and horned the ground and the vegetation and scent-marked low twigs. In both these cases, he was chasing a male-female pair. In one of these two cases the chaser was also observed repeatedly trying to mount the female.

7.3.2.6. Territorial marking Figure 7.6 shows the distribution of duiker latrines at IET superimposed on the ranges of collared duikers determined from sightings. If the area of the known ranges is divided into 25-metre squares and the number of squares with latrines and with range boundaries is calculated, a χ^2 test shows that latrines tend to occur along boundaries ($\chi^2 = 72.1$, 1 d.f.; $p < 0.001$). A notable exception is in the case of Mae Mae and Christiane who extended their range towards the east in the course of the study; two latrines were found in the middle of their range, and may have marked the range boundary before their range was extended.

In addition to marking with latrines, both male and female duikers were observed scent-marking on range boundaries (but not elsewhere). Males were also seen horning the vegetation and engaging in chasing and fighting on boundaries of ranges. No such behaviour was seen amongst females.

Figure 7.6
Distribution of duiker latrines at IET in relation to ranges.



KEY
□ Duiker latrine
—— Home range limit
x Individual pellet pile
G Sighting of Gabrielle (J♀)
~ Stream
- — Limit of area searched

0 100 200 metres

7.3.3. Discussion It has been shown that C. maxwelli live in small groups consisting of an adult male and one, or more rarely two, adult females with their offspring. This is reflected both in observations of radio-collared animals and in the size and composition of groups observed opportunistically - 85% of sightings were of one or two animals, and maximum group size was five. 83% of pairs were of male and female or female and young; 75% of threes were male, female and young. Larger groups were not simply aggregations of animals at food patches as has been suggested (Aeschlimann, 1963), since groups of four and five were observed at rest for periods of up to 25 minutes, and intergrooming between adults of the same sex was observed. Rahm (1961, in Aeschlimann 1963) also reports groups of up to four in the wild.

Radio-tracking data presented in Chapter 6 show that each group has a small, constant range, apart from occasional expeditions across neighbouring ranges by adult males and by juveniles. Both males and females mark range boundaries with both dung and glandular secretions; males also physically defend the boundaries against other males. Thus C. maxwelli is territorial. No evidence of territorial defence was seen by females, although Ralls (1975) reported that in captivity, a resident female will constantly pursue and displace a strange female introduced to the enclosure. Dubost (1980) cites cases of territorial defence by both females and males in free-living C. monticola even though in this species, unlike *C. maxwelli*, it is mainly the male which engages in scent-marking.

There is little mention in the literature of the use of latrines by duikers (except for *C. nigrifrons*, Plumptre, 1991). Dubost reports (1980, 1983) that dung was used for territorial marking throughout the territory by *C. monticola*, but there was no evidence of latrine areas on territorial boundaries. However, latrine areas have frequently been observed in captive animals, which use the space available to them in a very organised way. Aeschlimann (1963) found that captive *C. maxwelli* had two commonly-used rest sites, one latrine area, fixed marking points and well-trodden paths. My own observations at Monrovia Zoo, Liberia in January 1990 and of a captive black duiker during this study confirmed the use of latrines in captivity by *C. maxwelli*, *C. jentinki*, *C. niger* and *C. sylvicultor*, were inconclusive for *C. ogilbyi* and *C. zebra*, and showed a complete lack of latrines for *C. dorsalis*. In the present study, it was established that *C. maxwelli* used latrine areas to mark territorial boundaries. In addition there was a network of much-used trails, and within each tracking period, duikers would frequently be seen using the same trails at about the same times each day. The trails and patterns of movement changed in the course of a few months. It is possible that such changes reflected changes in availability of fruits, although notes of principal fruit patches showed no clear link. Sleeping places were changed almost every night, except in the case of infants.

The impression that *C. maxwelli* lives in small groups which are strictly territorial is complicated, however, by evidence of social interactions between neighbouring groups. The female Christiane and her juvenile daughter were seen repeatedly accompanying a neighbouring male-female pair for hours at a time in May to July 1991. The male Lucien temporarily joined a neighbouring pair which entered his territory after the death of his mate, Germaine, and was seen not only interacting aggressively with the strange male but also intergrooming with him. Lastly, the juvenile Sarah was seen on the border of her group's territory playing with two other juveniles of her own age. Observations are insufficient to define intergroup relationships at present, but a picture of a purely territorial animal living in isolated groups is insufficient. Dubost (1980) cites a case of an adult male *C. monticola* who returned to his natal territory after dispersal and who then continued to spend about half his time with his father. Such parent-offspring bonds may occasionally persist after the offspring reaches adulthood.

Group sizes reported for *C. maxwelli* are comparable to those reported by Dubost (1980) for *C. monticola* (80% of sightings were of singles or couples; 17.5% of threes), but larger than those reported by Crawford (1984) for the same species (98% of sightings were of singles or couples). Dubost claims that groups of three or four consisted of a male-female pair plus infant or juvenile offspring. It is often impossible to distinguish older juveniles from adults from a brief field sighting, and in the study reported here, larger groups probably included juveniles more often than was recorded. However this was not always the case; in particular, in the case of Lucbersone's group with two females, although one female was visibly older than the other, both appeared adult and as far as could be ascertained, both produced infants in February 1991.

For both C. monticola and C. maxwelli, group sizes are smaller than might be expected from the social systems reported, with a preponderance of single animals. There are two factors contributing to this; firstly, members of a group spent some time apart. The three couples of C. maxwelli in this study where both animals were tracked spent between 44% and 14% of the time in different hectare grid-cells. Secondly, even when animals were travelling 'together' along the same route they were often separated by a distance greater than the visibility limit in the forest; there could be a delay of up to three minutes between the sighting of one animal and the arrival of the next at the same point. Similarly, Dubost (1980) gives a mean distance of 45 - 75 m between the male and female of a pair of C. monticola, who spent only 40% of the time at a distance of less than 30 m. In many observations it is likely that additional animals travelling at such distances were not observed, especially if the first animal gave an alarm call. Such large inter-animal distances also raise the question of how animals stayed in contact and coordinated their direction of travel. Both C. maxwelli and C. monticola constantly flick their tails when active, show an eyecatching white flash of the underside of the tail with each flick. It is presumed that this is communicatory (Dubost, 1980), but it is invisible in thick undergrowth at distances of more than 25 to 30 m. It is likely that communication at greater distances is mostly olfactory, by means of both scent-marks placed actively on twigs with the preorbital glands, and secretions left by the pedal glands in the course of travel. The tail-flick signal may facilitate homing-in once the two animals are near each other.

The male followed the female in 63% of cases, which compares with 68% for C. monticola. This has also been reported for many other ground-living monogamous species (in Dubost, 1980). In C. monticola, mothers followed their offspring in 70% of cases.

7.4. Infant behaviour

7.4.1. Methods Records were kept of all sightings of infants or juveniles (the latter defined as young animals at least two thirds the shoulder height of the mother).

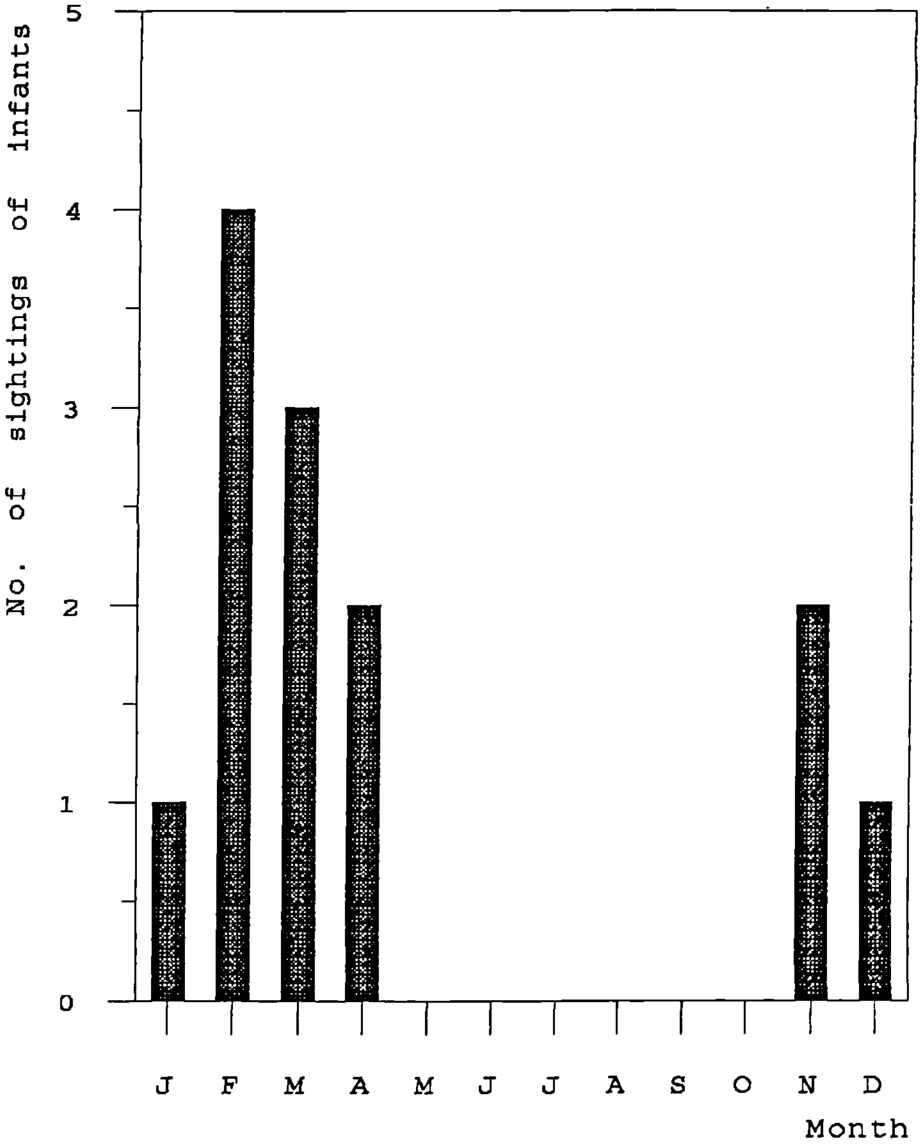
Behaviour and development of infants in the groups with radio-collared animals was monitored as closely as possible.

In early March 1991 an infant was seen lying up in Lucbersone's range, and was observed frequently over the following months. Watches were kept by an observer sitting half-hidden some 10 metres away from her until she left the bed some weeks later; during this time, she became partly habituated to the presence of an observer and later, when she was observed elsewhere, would sometimes stay in the presence of an observer without showing signs of alarm. Anecdotal observations made on the behaviour and development of this and other infants are summarised below.

7.4.2. Results Monthly numbers of sightings of infants are shown in Figure 7.7 (excluding repeated sightings of known individuals). Infants were seen only from November to April, indicating a well-defined birth season. During catches, four heavily pregnant females were caught, of which three were during the birth season, and one in July 1990 (see Appendix 5). One lactating female was caught at Gouleako in September 1991.

The infant in Lucbersone's range, which was named Sarah, was first seen on 3rd March 1991 and first fully described on 14th March 1991, when her age was estimated at 2-3 weeks. She habitually lay in a hollow in the leaf litter at the base of a tree 2 m to the side of a transect. She was discovered when flushed, when the observer was only 3 metres from her 'bed'. At first, the infant made only short forays from the bed to explore an area about 10 m in diameter and to eat dead leaves from the forest floor. An adult female duiker, assumed to be

Figure 7.7 Monthly numbers of sightings of infant Maxwells' duikers (February 1990 - November 1991)



her mother, often approached within 10 metres of the bed, when Sarah would run out to greet her; both would then disappear from view, and Sarah would return 15-30 minutes later. It was assumed that she was suckling at these times although suckling was never observed. Sarah was first seen far from the bed on 10th May 1991 (at an estimated age of two and a half months). By the end of May (aged three months) she had stopped using the bed, was eating green leaves, and was moving around Lucbersone's range extensively both by herself and in the company of adults from Lucbersone's group. At this time she was about two thirds the height of the mother, and was described as a juvenile.

Sarah was first seen eating fruits (Dialium aubrevillei (Caesalpinaceae) and Sacoglottis gabonensis (Humiriaceae) in July, aged 4 to 5 months. She was often seen with a juvenile male of her own age, who may have been the son of the second female in this group and was later seen with other members of the group. The male already had fully erupted horns. The two juveniles were observed to intergroom and to chase each other in play. Both were seen regularly in Lucbersone's range until the end of the study in December 1991.

Less extensive observations were made on an infant which was discovered lying-up at the base of a tree in November 1991. The infant was estimated to be one and a half to two and a half months old when first observed. Watches at its 'bed' showed a similar pattern of activity to Sarah at that age, with increasingly long absences from the bed until it was completely abandoned by mid-November.

Infants were born to two other radio-tracked groups at IET at the same time as Sarah, and although they were seen less frequently, their rate of growth and the degree of independence from their parents were similar to that observed for Sarah.

7.4.3. Discussion Aeschlimann (1963) reported from anecdotal observations of C. maxwelli by hunters that births occur all the year round, but there is a main birth season in the main dry season from January to March (the time of maximum fruit abundance), and a minor birth season in August. The present study found strong evidence for seasonality of births over a slightly wider season. Infants, aged one to three months, were seen only in November to April. Aggressive behaviour between males was most frequently observed from April to July, suggesting a rutting season at this time. Additionally, one female near parturition was caught in July, and one lactating female in September. The end of gestation and the time immediately after birth are key stress points in the reproductive cycle. Dubost and Feer (1992) found a comparable pattern, with year-round births peaking in the time of maximum availability of edible fruits, in four other frugivorous forest ruminants - C. monticola, C. dorsalis, C. callipygus, and H. aquaticus. Another stress-point is at the time of weaning. Both in the present study and for the four species cited above, this is during a period when fruit are scarce but young shoots and buds are plentiful. It may be in adaptation to this that juveniles are more folivorous than adults (See below and Chapter 5; also Dubost, 1980; Feer, 1988; Dubost and Feer, 1992).

Like many ungulates, in C. maxwelli the newborn infant lies hidden for the first few weeks of its life and is visited by the mother for suckling, when she calls it from its 'bed' as she approaches (Jarman, 1974; Estes, 1974). C. maxwelli infants usually lie at the base of a tree, often between buttress roots (personal observation and Aeschlimann (1963)), and when approached by a person stay immobile until a distance of three metres or less is reached. The same bed can be used for a month or more, and a visible hollow develops in the leaf-litter. The young duiker begins to eat dead leaves from the forest floor at an age of about two weeks, and from about four weeks it begins to venture away from the bed to forage. At first it stays near the bed and returns frequently, always coming back to spend the nights there, but by three months the bed is completely abandoned and the juvenile moves through the territory of the parents, either alone or with other members of the parental group. Dubost and Feer (1992) cite two to four months as the age when weaning occurs.

The juveniles of the groups radio-tracked in this study were only about 10 months old when the study finished and were all still in their parents' territories, so it was not determined at what age young animals emigrate from the parental territory. One juvenile female with a radio-tracked group in the first year of the study was not seen in the second year, and may have emigrated or died. In C. monticola, Dubost (1980) reported that 69% of young emigrated - females at an age of 1 - 1.5 years, and males at about 2 years. All females and most males who stayed in the parental territory as adults were in groups where the parent of the same sex had died or emigrated; thus no groups were formed which contained two adults of the same sex.

7.5. Conclusions

The data presented in this chapter make it possible to compare C. maxwelli with what is known of the social ecology of other duiker species, and confirm that in many aspects it resembles C. monticola. Both species are diurnal and live in small groups within territories which are marked by glandular secretions (and latrine areas in the case of C. maxwelli), and defended against neighbouring groups. Territories are stable over a number of years and have minimal overlap with other groups. Infants lie concealed from predators for the first few weeks of life and are visited by the mother for suckling. However, there are certain differences between the two species. Although both are principally monogamous, this is not always the case for C. maxwelli. In this study, one group out of three at IET was polygynous, consisting of a male and two adult females which were both reproducing; in addition, males were seen chasing neighbouring females, and in one case a male was seen fighting a neighbouring male in order to mount a neighbouring female. The slightly higher proportion of females than males also suggests a low level of polygyny. Dubost marked 171 C. monticola and radio-tracked nine individuals over a period of five years, yet he saw no such evidence of polygamy or promiscuity. Territorial aggression was observed only between male C. maxwelli, whereas in C. monticola both sexes defend the territory against outsiders of their own sex. No groups of C. monticola were found with more than one adult female; Dubost suggests that a territory could not support groups larger than monogamous family units. The tendency towards polygamy in C. maxwelli is also suggested by captive studies, which show that a male can be kept with three or four breeding females with acceptably low levels of aggression (Aeschlimann, 1963; F. N'Golo, Abidjan Zoo, personal communication.).

Although duikers have long been classified as monogamous (eg. Jarman, 1974), it has become apparent that there is a range of mating systems among different duiker species. C. monticola is monogamous but C. callipygus and C. dorsalis are both polygynous; in the former species two females may share the same range with a single male, whilst in the latter, a male may have a territory covering those of two neighbouring females (Feer, 1988). The mating system of C. maxwelli is in between the strict monogamy of C. monticola and the polygyny of the larger species. It is probable that the mating system found for particular individuals will reflect factors such as territory size and quality, habitat quality, and population size and structure.

CHAPTER 8. POPULATION DENSITIES

8.1. Introduction

In this chapter, results are presented on the presence or absence of duiker species in the two study sites and estimates of their population densities. Estimated densities will be used in Chapter 9 together with data on births, deaths and age-sex ratios (from Chapter 7) to look at population dynamics of C. maxwelli and the potential for wildlife management.

A number of methods have been developed for the estimation of mammal populations in forests, both from direct observations of animals and from records of their tracks and dung (eg. Barnes and Jensen, 1987; Davies, 1989; A. Dunn, unpublished; Koster and Hart, 1988; Wilkie, 1987; Wilkie and Finn, 1990). Attempts have been made in the last five years to estimate populations of duikers in dense forest (Davies, 1989, 1991; Hart and Hart, 1989; Koster and Hart, 1988; Lahm, 1993; Plumptre, 1991; Prins and Reitsma, 1989; Wilkie, 1987, 1990), but each method has its own biases and it is hard to obtain a baseline against which to test accuracy. It has been suggested that radio-tracking may be the best method, but it is too expensive and labour-intensive to be used for basic surveys. In the present study, a range of population census methods was used in parallel with a radio-tracking study, in order to assess their accuracy and identify the most useful methods for basic surveys.

Data for transect censuses of both dung and duikers in 1991 were collected by Gle (1993), and are further analyzed here for comparison with other methods.

8.2. Methods

8.2.1. Transect censuses of duikers Transect censuses were carried out as described in Burnham et al (1980) (See also Appendix 8(a) for summary of theoretical background). Existing transects within the study grid at each site were walked in the mornings between 0600 and 1300 and on moonless nights between 2200 and 0500 by one or two people, at a rate of about 1 km per hour. Care was taken to walk quietly and to watch ahead and to the sides for signs of duikers. (At night, a strong head-torch was used to see the orange reflection from their eyes). When a duiker was seen or heard, the perpendicular distance from the transect on contact was estimated in metres, the location, time and habitat were recorded, and where possible, the species, age class and sex of the animal was noted. A Hewlett-Packard 32S pocket calculator was programmed to allow analysis in the field using a Fourier model. Later, a more complete analysis was carried out with the program DISTANCE, which presents alternative models and gives various options to improve the data fit (see Appendix 8(b) and Laake et al, 1993). Results from day-time and night-time censuses were analyzed separately.

8.2.2. Transect censuses of dung Given the mean number of dung-piles produced by one animal in a day (defaecation rate,

d) and the daily rate at which dung-piles decay (decay rate, r), the population density can be estimated from the density of dung-piles (Y) as follows:-

Population density $P = (Y \times r)/d$.

(Barnes and Jensen, 1987).

Defaecation rates are given by Koster and Hart (1988) as 4.9 and 4.4 pellet groups per day for the blue and bay duikers (C. monticola and C. dorsalis) respectively. The animals' diet consisted of sweet potato leaves and ad lib. quantities of each of four different species of wild fruit in turn; the defaecation rates correlated directly with the amount of fibre in the diet. According to my observations during three weeks at Monrovia zoo from 24th December 1989 to 12th January 1990, defaecation rates were almost constant at three piles a day for C. dorsalis, C. zebra and C. sylvicultor. Their diet consisted of sweet potato leaves, "grain dust" (husks from hops). A captive black duiker kept in an enclosure in the forest during the present study and fed on sweet potato leaves, yam roots and varying quantities of miscellaneous forest fruits had a mean defaecation rate of six piles a day (range 2 to 12, s.d. 1.57) over a period of nine months.

No figures on defaecation rates were available for C. maxwelli, but the variation between the above figures is greater between studies (probably due to differences in diet) than between species. A mid-range value of 4.5 piles per day was used for the present analyses, which is in line with the values selected by Koster and Hart (1988) as realistic for animals in the wild.

Decay rates can vary greatly between habitats and between seasons (Koster and Hart, 1988; Davies, 1989; Nummelin, 1990; Wilkie and Finn, 1990). In order to determine decay rates, fresh pellet groups were located every few days at each site, starting at least a month previous to each pellet count. They were marked with fluorescent tape and re-visited periodically in order to determine the length of time until they disappeared (which was taken as the time when less than four pellets could be found). A mean number of days ($\bar{d}$) until disappearance was calculated for each sample, and the decay rate was taken as $1/\bar{d}$ piles per day.

Density of pellet groups on the ground was estimated by transect censuses involving two people, following the method of Koster and Hart (1988). They were carried out in 1990 as the trail systems were cut, and again in 1991 from existing trails. A 30 m tape was laid along the trail and taken as the centre of the transect. Both people then walked along the transect at a rate of about 10 m per minute, bent over to search the ground thoroughly along the transect and to either side for pellet groups. When a pellet group was found, the perpendicular distance from the transect centre to the centre of the pellet group was measured, and the location and habitat were noted. Only pellet groups with four or more pellets were counted. Estimates of pellet group density were carried out as for transect censuses of duikers (see above and Appendix 8), and were used to estimate duiker densities as outlined above. Initial studies at Monrovia Zoo in December 1990 to January 1991 had found that pellets could not be identified to the species of duiker; only small duikers (C. dorsalis, C. maxwelli, C. niger, C. ogilbyi and C. zebra) and large duikers (C. sylvicultor, C. jentinki) could be distinguished. Since no large pellets were found during transect censuses, population density estimates are for the small species only.

8.2.3. Net-capture During day-time duiker catches, nets were used to encircle 1 ha blocks of forest (see Section 2.4 for method). This was done at IET between March and June 1990, and at Gouleako between July and October 1990. Following Davies (1989), population densities were estimated from the frequency of encounter with duikers during such catches.

8.2.4. Estimates from radio-tracking Radio-tracking was used to estimate home-range sizes of Maxwell's duikers at each study site (See Chapter 6). Population densities of this species were then estimated by extrapolation from home-range sizes and degrees of overlap, together with the number of animals using each home range.

8.2.5. Other methods Additional methods were piloted during the present study in conjunction with D. Gle (reported in more detail in Gle, 1993). A modification of the capture-recapture method was attempted at the IET site at the end of the radio-tracking study. Point censuses were conducted by sitting still in inconspicuous locations in the forest for

10 to 20 minutes, both by day and by night. Nasal calls used by hunters were used to attract duikers in to the callers. In addition, all chance encounters with duikers other than C. maxwelli were recorded throughout the study. Concurrently, Gle (1993) carried out a brief survey of animals killed by hunters in late 1991.

8.3. Results

8.3.1. Transect censuses of duikers For day-time censuses at IET, a total of 32.779 km was walked over 15 days between 20th July 1991 and 5th December 1991. Forty-one sightings of duikers were made, giving an overall encounter rate of 1.25 per kilometre. Fourteen sightings involving 20 animals were of C. maxwelli (giving a mean group size of 1.4); five sightings involving five animals were of C. dorsalis; one was of C. niger, and one of C. ogilbyi. In the remaining 20 sightings, the species of duiker was not determined. Population density was estimated for the total data set as 36 animals km^{-2} (95% C.I. 24 to 56). (see Appendix 8(c) for details of analysis). However, the frequency of observations near the transect line was lower than that at greater distances (see Figure 8.1 in Appendix 8), suggesting that the duikers were either avoiding the line itself, or were moving away from the observer before being seen. This would cause the estimate to be artificially low (Buckland et al, 1993).

At Gouleako, 8.5 km were walked over five days without a single sighting of a duiker, so this method was abandoned.

Its failure was undoubtedly due to the thick undergrowth, which limited visibility to less than two metres in some habitat types (see Chapter 3).

For night-time censuses at IET, 23.283 km were walked over 10 days between 8th August 1991 and 11th November 1991. There were 46 encounters with duikers, making a mean encounter rate of two per kilometre walked. Thirty encounters involving 43 animals were of *C. maxwelli* (mean group size 1.4); six involving six animals were of *C. dorsalis*; in the remaining ten encounters, species were not identified. Overall density of duikers was calculated as 101 (95% C.I. 68 to 150); density of *C. maxwelli* alone came out as 102 (95% C.I. 58 to 179), because most of the unidentified observations were at great distances and therefore made little difference to the estimate.

At Gouleako, pilot studies proved that night censuses were ineffective because of the thick undergrowth.

8.3.2. Transect censuses of dung

Decay rates The mean number of days taken for dung piles to decay is given below for each site and each sample time (Table 8.1). At IET, they were similar in different habitats. At Gouleako it was not possible to take a large enough sample to treat each habitat separately, but there was no obvious distinction between habitats.

All decay trials were between June and October. Contrary to the findings of Nummelin (1990), decay rates were not inversely proportional to monthly rainfall (compare Table 8.1 with rainfall data in Appendix 3), but heavy rains had a major effect on decay rates. For example, in the latter half of 1990 the first heavy rains fell at the beginning of September. Fresh dung piles were washed away by the rains, although older piles remained. Thus the mean decay time for August was 41.19 days, whereas that for September was only 18.33 days. It is important that separate decay rate trials are carried out for each pellet census, and they should preferably start about a month before the census.

Table 8.1 - Mean decay time for dung piles at IET and Gouleako.

Site	Date	Habitat	Mean Decay Time	Sample Size
IET	6/91	FH	8.56 (s.d. 8.41)	17
IET	6/91	BF	9.40 (s.d. 4.28)	5
IET	7/91-8/91	FH	23.73 (s.d. 16.6)	74
IET	7/91-8/91	BF	23.10 (s.d. 15.9)	22
GOU	8/90		41.19 (s.d. 14.83)	31
GOU	9/90		18.33 (s.d. 15.15)	18
GOU	7/91		11.70 (s.d. 8.75)	27
GOU	8/91		16.58 (s.d. 19.43)	31
GOU	9/91-10/91		16.50 (s.d. 3.96)	8

Below are the months in which transect censuses of dung densities were carried out, together with the decay rates used for further analysis:

IET	February to March 1990. No decay trials leading up to census since researchers had only just arrived at study site.
IET	July to August 1991. Decay time 23.73 days (s.d. 16.60). Taken from July to August since June time too short to affect census.
Gouleako	July to August 1990. Decay time 44.64 days (s.d. 14.83). Taken from August (no data for July).
Gouleako	August to November 1991. Decay time 14.58 (s.d. 14.57). Taken from July to October.

Pellet transect censuses and duiker population density estimates The details of analysis of transect data for each site in each year are given in Appendix 8(e). Taking the defaecation and decay rates given above, the resultant estimates of duiker population densities are as follows:

IET, 1990 - Assuming a decay time of 60 days since this is the driest time of year,

$$\text{Population density } P = (19{,}267 \times 1/60) / 4.5$$

$$= 71 \text{ duikers km}^{-2}$$

(95% C.I. 16 to 318)

IET, 1991 - Could not model transect data. Density estimate not possible (see Appendix 8(e)).

Gouleako, 1990 - $P = (74,612 \times 1/44.64) / 4.5$

$= 371$ duikers km^{-2}

(95% C.I. 192 to 698)

Gouleako, 1991 - Could not model transect data. Density estimate not possible (see Appendix 8(e)).

8.3.3. Net-capture Forty-eight ha were encircled with nets at IET, in seven of which duikers were encountered. The species seen were as follows:

6 C. maxwelli

2 C. dorsalis

1 C. ogilbyi

2 C. spp. (unidentified).

This gives an estimation of overall duiker population density of 23 duikers km^{-2}, and for C. maxwelli of 13 km^{-2}. However, the average encounter rate dropped from one hectare in four to one in six after the first 12 drives, then stayed constant. At Gouleako, there were three encounters in a total of eleven hectares searched. Each encounter was with a male-female pair of C. maxwelli. This gives a population density estimate of 55 C. maxwelli km^{-2}.

8.3.4. Estimates from radio-tracking Radio-tracking of C. maxwelli revealed that home ranges averaged 5 to 6 ha at IET and 3.6 ha at Gouleako (see chapter 6). Of the three groups tracked at IET, two consisted of an adult pair, and one of a male with two females. Each female had an infant early in the year, and in one group a juvenile was also present. One juvenile, Gabrielle, belonged to none of these groups but had a home range overlapping with all three and including an exclusive area of about 1 ha. Thus, taking a mean home range area of 5.5 ha, in a total of 17.5 ha there were eleven Maxwell's duikers - seven adults, two juveniles, and three infants. Multiplying up, this gives a density of **63 *C. maxwelli* km^{-2} at IET**.

Group size at Gouleako could not be checked because of poor visibility, but net catches of *C. maxwelli* were mostly of monogamous pairs. We will assume a similar group size and proportion of infants and juveniles to those at IET, with 11 individuals in three home ranges. The population density in habitats used would be 11 in 3 x 3.6 ha, or 98 km^{-2}. Taking into account that fields and bamboo stands were not used and covered 19% of the site, the overall density of *C. maxwelli* at Gouleako would be 98 x 81/100 = **79 km^{-2}**.

8.3.5. Other methods Capture-recapture proved too time-consuming and labour-intensive to catch a sufficiently large number of animals for an estimation of the population. Observations from fixed points by both day and night were infrequent, although the number of sightings was increased if simple hides were used, especially by latrine areas. The nasal call used by hunters to attract duikers gave better results; in 1990 at IET, duikers approached in response to three of nine calls (twice a Maxwell's duiker and once a bay duiker). All came within 3 m of the caller, allowing sex and age-class to be determined. At night, two of six calls attracted duikers (one Maxwell's and one bay). In 1991, duikers responded to seven of eighteen day-time calls (six *C. maxwelli*, one *C. dorsalis* and one unidentified red duiker).

Table 8.2 - Opportunistic sightings of duikers other than *C. maxwelli* at IET

Species	Group size	Number of sightings in different habitats			
		FH	BF	Other	Total
By day:					
C. dorsalis					14
	1	5	7		
	2	1	1		
C. ogilbyi	1	5	4		9
C. zebra					6
	1	1	2		
	2	3			
Unidentified "red" (above 3 species)	1	3	1		4
C. niger	1	4	3		7
C. sylvicultor	1			1	1
By night:					
C. dorsalis					21
	1	7	12		
	2	1	1		

The numbers of chance encounters at IET for each duiker species except *C. maxwelli* are given in Table 8.2. All species under 25 kg body weight were seen in both FH and BF in the mature forest at IET. The larger *C. sylvicultor* was seen only in secondary vegetation. Tracks over 60 mm long, which must be of either *C. sylvicultor* or *C. jentinki*, were twice recorded. C. jentinki was seen within 3 km of the study site during the course of the study and may have been an occasional visitor to the study area.

At Gouleako, only C. maxwelli, C. dorsalis (once) and C. niger (seven times) were seen, although villagers claimed that all duiker species raided the fields except C. jentinki. Large duiker footprints were recorded and assumed to be those of C. sylvicultor.

Gle (1993), in interviews with villagers in July to December 1991, recorded duikers caught as follows:

17 C. maxwelli (13 shot, 4 snared)
5 C. ogilbyi (2 shot, 3 snared)
3 C. dorsalis (2 shot, 1 snared)
3 C. niger (2 shot, 1 snared)
2 C. zebra (2 snared)

Similarly, duiker stomach contents gathered from hunters were of 8 C. maxwelli, 2 C. dorsalis, and 1 C. ogilbyi.

8.4. Discussion

Table 8.3 summarises population density estimates by the various methods used.

Estimates for IET vary between 23 and 102 individuals km^{-2}. At Gouleako, net capture and radio-tracking estimates are close (55 and 79 individuals km^{-2} respectively), but the estimate from pellet group transects is more than five times as great, at 396 animals km^{-2}. For day-time censuses, all species of duiker were taken together; pellet counts refer only to the five smaller species, since no tracks of C. jentinki or C. sylvicultor were found during censuses. Radio-tracking data are for C. maxwelli only.

Table 8.3 - Estimates of population densities of Cephalophus spp. by different methods[1]

Method of estimation	IET	Gouleako
Day-time transect of duikers (1991)	36 (24-56)	-
Night transect of duikers (1991)	101 (68-150) C. maxwelli: 102 (58-179)	-
Pellet group transects (1990)	71 (16-318)	396 (217-723)
Net capture	23 C. maxwelli: 13	C. maxwelli: 55
Radio-tracking (C. maxwelli only)	63	79

[1] Figures are per km^2. Figures in brackets give the 95% Confidence Intervals.

8.4.1. An Evaluation of census methods

8.4.1.1. Transect censuses of duikers

Day-time The estimate given for IET in Table 8.3 is just over half that given from radio-tracking data, which matches the finding of Dubost (1980) that transect censuses of the blue duiker (C. monticola) produced density estimates of only about half the true values, probably because of avoidance behaviour by the animals. Figure 8.1 (a) in Appendix 8 suggests that many animals moved away from the transect before being seen, since there were few observations close to the transect centre. This was borne out by field observations; many encounters with duikers consisted only of a fleeting glimpse when the observer's attention was drawn by an alarm call as the duiker fled. Similarly, there were occasions apart from censuses when a duiker would be seen hurrying past, to be followed after a short interval by another researcher, who was unaware of the animal fleeing ahead. In attempts to approach radio-collared animals while listening to their signals, it was found that some individuals were consistently moving away before they were seen (see also section 2.6). Davies (1991) and Plumptre (1991) reported similar observations. This behaviour violates one of the key assumptions of the theoretical background to line transect censusing, and should result in an underestimate. The effect may change with sampling effort, especially if transects are used repeatedly, so it is not possible to use a conversion factor to estimate true densities.

Night-time The estimate given in Table 8.3 for C. maxwelli from night transects at IET is rather high compared with radio-tracking densities, although the latter does fall within the 95% confidence intervals. Figure 8.1 (b) in Appendix 8 shows no evidence that animals moved away before detection and this was supported by field observations. Once seen, animals were dazzled with torchlight and usually stayed still, allowing ample time for distances to be calculated. Radio-collared animals did not usually move from the time the signal was detected until the time when they were seen (except one juvenile female - see section 2.6), unless they were a long way from the paths and the observers made a lot of noise in approaching them through the undergrowth. C. dorsalis, which is nocturnal, moved away more often but still less so than in the day-time. Thus this method is preferable to day-time censuses for C. maxwelli. Additional advantages are the higher encounter rate (2 encounters per km in contrast to 1.25 encounters per km in the day-time), and the fact that it was more often possible to approach close enough to determine species, sex and age-group of the animals.

8.4.1.2. Transect censuses of dung At Gouleako, the 1990 estimate from pellet transects was more than five times as high as the radio-tracking estimate. Pellet transects gave the estimate closest to that from radio-tracking data at IET, but the variance and the 95% confidence intervals were so large as to make the estimate almost meaningless. There are many potential sources of error in the estimates. Apart from the difficulty of distinguishing dung of different duiker species, and the variability of defaecation rates (ranging from 3 to 6 piles per day - a factor of 2) and decay rates (averages per month ranging from 8 to 45 in the present study, making sizeable pilot studies necessary for every census), dung piles were loosely grouped in latrine areas (see also Chapter 7). Theoretically, each latrine area should be quantified and the mid-point identified, so that censuses of latrines could be carried out rather than of individual pellet groups. However, since latrines can be over 30 m across and consist of over 100 pellet groups, this would be prohibitively time-consuming.

A look at the histograms of pellet piles found at different perpendicular distances from the transect indicates further sources of error with the method (See Appendix 8, Figure 8.2). Transect census modelling assumes that the likelihood of detection decreases relatively smoothly with increasing distance from the transect, but in none of the data sets did this seem to be the case. Data for 1991 were particularly far from this assumption, which was why it was impossible to model them using transect census models. Possible confounding factors for 1991 include atypical pellet decay rates on the transects, which tended to be clear of leaf litter and, in secondary habitats, more exposed than the surrounding ground; use or avoidance of transects by duikers; and extreme differences in detection frequency on the relatively clear transects and in the surrounding undergrowth. White (1992) found that animals tended to use existing transects, which would result in an overestimate of population densities.

8.4.1.3. Net-captures The figure for IET from net-captures is extremely low. Encounter rates decreased with sampling effort, and only C. maxwelli were seen after the first 12 drives. It is likely that duikers learned to avoid the drives even though the team of catchers improved the speed and quietness with which they could put up the nets. Once, two C. maxwelli were seen leaving a 1 ha block as nets were erected around it. However, it was found from radio-monitoring that in the greater cover provided by thick secondary vegetation at Gouleako, C. maxwelli were more inclined to freeze than to run while the nets were being erected; thus, there was less bias from avoidance behaviour. The density estimate for C. maxwelli at Gouleako given in the above table was close to the estimate from radio-tracking. However, no other duiker species was encountered during netting at Gouleako, although they were known to be present from tracks, occasional opportunistic sightings, and reports from villagers.

8.4.1.4. Estimates from radio-tracking The density of C. maxwelli within a 17-ha area of the forest at IET was determined with a high degree of accuracy, and extrapolation leads to a density of 63 individuals km^{-2}. At Gouleako, estimation was less certain since an assumption had to be made that group size within each home range was the same as at IET.

8.4.1.5. Other methods Hunters' calls may be valuable for quick surveys to determine the presence or absence of different species, and deserve further research to determine whether they could be used to assess changes in duiker populations. It is reported that hunters in some parts of Africa have slightly different calls for different species of duiker (eg. F. Feer, personal communication).

8.4.1.6. Recommendations All the methods described above for estimating population densities have some drawbacks. Radio-tracking is probably the most accurate method but is expensive and time-consuming. For basic surveys, interviews with local people, opportunistic sightings (including from hides) and the use of hunters' calls are likely to be the quickest ways to determine the presence or absence of different species. For a more detailed look at populations in forests, night censuses are the most free from known factors of bias, and the least time-consuming. In secondary vegetation, net-captures and pellet counts are the only options. Net-capture is labour-intensive and causes disturbance both to animals and to the vegetation, but is probably the most reliable method. Pellet counts, preceded by dung decay trials, should be used alongside net-capture, to further investigate the sources of error.

8.4.2. Population densities of duikers Table 8.4 summarises population densities given in the literature on forest duikers at a number of sites in Africa.

Table 8.4 - Duiker population densities from other studies

Site and Habitat	Species	Method	Density km^{-2}	Ref
near Makokou, Gabon (lowland rain forest)	C. monticola	Capture-recapture	62-78	6
		Transects	21-31	
	C. dorsalis	Net capture	>15	5
	C.callipygus		>20	
	C. dorsalis	Radio tracking	10.7	7,8
	C.callipygus		7.1	
NE Gabon (lowland rain forest). Figures for hunted/unhunted areas.	C. monticola	Night transects	30/53	12
	C.callipygus		0.6/6.3	
	C. dorsalis		2.5/6.8	
Lowland coastal rain forest, Gabon	C. sylvicultor + Tragelaphus scriptus	Tracks	0.26	14
	All duikers < 30 kg + Neotragus batesi + Hyemoschus aquaticus		0.53	
Lope, Gabon (lowland rain forest). Logged and unlogged forest	All duikers	Transect	5.1	16
	C. monticola	Pellet transects	3.7 - 13.1	16
	"Red" duikers		3.5 - 15.7	16
	C. sylvicultor		0 - 4.5	16
Ituri, Zaire (Lowland rain forest) - Hunted	All	Drive counts	25.1	10
	"Red" duikers		7.4	9, 10
	C. dorsalis		1.5	
	C. callipygus		3.2	
	C. nigrifrons		0.6	

Table 8.4 - Duiker population densities from other studies

	C. leucogaster		2.7	
	C. sylvicultor		0.7	
	C. monticola		14.9	
Ituri Zaïre (lowland rain forest). Figures for regrowth/climax	C. monticola	Pellet counts	67/59	17
	"Red" duikers		49/81	
Karisoke, Rwanda (Montane rain forest)	C. nigrifrons	Transects	5-25	13
South African evergreen coastal forest	C. monticola	?	130-238	2
	C. natalensis		40-80	
Gola, Sierra Leone (Lowland rain forest) - logged + unlogged	All	Drive counts	40-50	3
	C. maxwelli		15-30	
	"medium size" (C. niger, C. dorsalis, C. zebra)		15-30	
As above, unlogged	Medium size	Transects	8	
As above, logged			1	
As above, farmbush	C. maxwelli		2-3	
Eastern Liberia (lowland rain forest)	C. jentinki	?	1	11
	All except large spp.	Pellet transects	14	4
Forest reserve, Ghana (lowland rain forest)	C. maxwelli	?	0.31	1
Marahoue, Côte d'Ivoire (Guinean *savanna* with gallery forest)	C. maxwelli	Transects	2.7	15
	C. rufilatus		2.0	

Table 8.4 - Duiker population densities from other studies

Comoe, Côte d'Ivoire (Sudanean savanna with gallery forest)	C. maxwelli		0.5	
	C. rufilatus		1.3	
	C. sylvicultor		0.1	

References for Table 5.4:- 1 Bourliere (1963, in Dubost, 1980); 2 Bowland, 1990, in F. Feer, in press; 3 Davies, 1991; 4 A. Dunn, unpublished manuscript; 5 Dubost, 1979; 6 Dubost, 1980; 7 Feer, 1988; 8 F. Feer, in press; 9 Hart, 1985; 10 Hart and Hart, 1989; 11 Kranz, in East, unpublished manuscript; 12 Lahm, 1993; 13 Plumptre, 1991; 14 Prins and Reitsma, 1989; 15 Roth and Hoppe-Dominik, in East, unpublished manuscript; 16 White, 1992; 17 Wilkie and Finn, 1990.

Variations in density estimates are likely to reflect both true differences in duiker densities and differences in methodology; however, a number of interesting comparisons are possible. C. maxwelli population densities were estimated from drive counts (equivalent to net captures) at 15 to 30 km^{-2} in the Gola forest, Sierra Leone and at 2 to 3 km^{-2} from day-time transects at farmbush nearby (Davies, 1991). In the present study, net captures gave densities of C. maxwelli at 13 km^{-2} in the forest (believed to represent a true density of about 63 km^{-2}) and 55 km^{-2} in mixed secondary growth at Gouleako. Gola forest is widely hunted, and a visit by the author to Gola during Davies' study gave the strong impression that duiker densities were far lower than in Taï since all signs of duikers were rare. However, the undergrowth in the forest is thicker than at Taï (personal observation), and drive counts may therefore have been less affected by avoidance behaviour by duikers. The farmbush studied at Gola was mostly secondary vegetation at a stage corresponding to JF2 and JBF in the present study; it was thus dissimilar to the site at Gouleako.

The estimate of duiker density is extremely low, which may be in part due to hunting, but also to poor visibility during transect censuses.

Other estimates of C. maxwelli are of limited value. Dubost (1980) referred to a study by Bourlière which cited a density of 0.31 km^{-2} for a forest reserve in Ghana, but details and methodology were not given. Figures for Marahoue and Comoe National Parks in Côte d'Ivoire were averaged out over gallery forest and large areas of savanna, where C. maxwelli would not be found. However, there are a number of estimates for the sister species C. monticola. Dubost (1980) cited a figure of 62 to 78 individuals km^{-2} from an extensive capture-recapture study carried out over three years in lowland rain forest in Gabon, and added that transect censuses gave about half this value (21 to 31 km^{-2}). Lahm (1993), also in lowland rain forest in Gabon, used night transects to estimate densities of 30 and 53 individuals km^{-2} for hunted and unhunted areas respectively. White (1992) found rather low densities (3.7 to 13.1 km^{-2}) from pellet transects in Lope, Gabon. In the Ituri forest in Zaïre, which is heavily hunted, Hart (1985, and Hart and Hart, 1989) estimated 14.9 C. monticola km^{-2} from drive counts, whilst Wilkie and Finn (1990) found densities of 67 and 59 km^{-2} in regrowth and climax forest respectively, from pellet counts. The high density of 130 to 238 individuals km^{-2} given for South African evergreen coastal forest by Bowland (1990, in F. Feer, in press) could indicate that population densities are far higher, especially since only two species of duiker occur there, but it would be interesting to know the method used to gain these figures.

In almost all studies where numbers are available, the small duikers (C. maxwelli in West Africa and C. monticola in Central and Southern Africa) are the most numerous. In Gola, drive counts suggested that C. maxwelli made up 50% of total duiker numbers. If we assume that C. maxwelli make up about 50% of the duiker population at the IET site at Taï, the total duiker population would be about 126 individuals km^{-2}. This is close to the estimate gained from night transect censuses. For C. monticola, the percentages found were 63 (Ituri, Zaïre, by drive counts; Hart, 1985, Hart and Hart, 1989); 58 (Ituri, regrowth forest, by pellet counts; Wilkie and Finn, 1990); 67 (Gabon, compared with only C. callipygus and C. dorsalis, by capture-recapture and net capture; Dubost, 1980), 91 and 80 (Northeast Gabon, in hunted and unhunted areas respectively, compared with only C. callipygus and C. dorsalis by night transects; Lahm, 1993). Only in White's study (1992) are the percentages for C. monticola considerably lower, varying from 4.2% in forest logged 20 to 25 years previously to 24.6% in forest logged only 3 to 5 years ago.

Estimates for medium-size duikers (15 to 30 kg) are generally much lower. Densities of C. dorsalis and C. callipygus were estimated near Makokou in Gabon at between 7 and 20 km^{-2} (net capture, Dubost, 1979; radio-tracking, Feer, 1988, in press). At Lope in Gabon, pellet transects gave estimates for all "red" duikers (C. dorsalis, C. callipygus, C. leucogaster, C. nigrifrons) together as 3.5 to 15.7 km^{-2} (White, 1992). In Ituri, the figure for "red" duikers was 8.0 km^{-2} by net captures (Hart, 1985; Hart and Hart, 1989) but 49 and 81 km^{-2} in regrowth and climax forest respectively by pellet transects (Wilkie and Finn, 1990). Hart (1985) found that the densities of *C. callipygus* and *C. leucogaster* were inversely proportional, suggesting some degree of competition between the two. In Karisoke, Rwanda, the only duiker present was *C. nigrifrons*, at 5 to 25 km^{-2} (day-time transects, Plumptre, 1991). In Gola, Sierra Leone, medium size duikers included *C. niger*, *C. dorsalis*, and *C. zebra*, with a combined density estimated at 15 to 30 km^{-2} (drive counts, Davies, 1991). No density estimates for the largest species, *C. sylvicultor* and *C. jentinki*, are above 1 km^{-2}, except in one site in logged forest at Lope (pellet transects, White, 1992).

The data suggest that the relative abundance of species in mature forest, in decreasing order, was *C. maxwelli* > *C. dorsalis* > *C. ogilbyi* > *C. niger* > *C. zebra* > *C. jentinki*, with *C. sylvicultor* absent from this vegetation type. In secondary forest, the order was *C. maxwelli* > *C. niger* > *C. dorsalis* > *C. sylvicultor*, with the presence of *C. zebra* and *C. ogilbyi* in doubt, and *C. jentinki* probably absent.

CHAPTER 9. DISCUSSION AND CONCLUSIONS

In this chapter, material from the previous chapters will be brought together to summarise the ecology of duikers at Taï in forest and secondary vegetation. Firstly, differences in food available in the two habitats will be described and possible effects on terrestrial frugivores and folivores will be discussed. Secondly, the ecology of the seven species of duiker will be summarised, and their ability to survive in secondary vegetation will be assessed. Subsequently, population dynamics of C. maxwelli at Taï and the likely effects of hunting will be outlined. Finally, conservation priorities for duikers and the potential for sustainable hunting or farming will be discussed.

9.1. The effects of food availability in mature forest and secondary vegetation

Wilson and Johns (1982) studied the effects of logging on animals in Indonesia and found that although there was a drop in mammal species diversity immediately after logging, many species would return to the area within three to five years, provided that there was undisturbed forest nearby. This was certainly the case in the IET site, which had been logged in the 1970's. All large mammal species commonly found in comparable unlogged forest nearby were present. Population densities were not studied in unlogged forest, but encounter rates in the study area and in unlogged areas were similar. Plumptre (1994) found that population densities of blue duiker (C. monticola) in the Budongo forest, Uganda, were similar in logged and unlogged forest.

Both total fruits and fruits potentially edible by Maxwell's duiker were less plentiful in the more disturbed mature forest at Gouleako (Chapters 4 and 5) than at IET, but even disturbed mature forests had significantly more fruits than secondary habitats. Mature forest at Gouleako had fewer mature trees than at IET and a lower proportion of some tree species which were harvested commercially or for local building materials. Some species harvested, such as Diospyros spp., are an important source of food for duikers. In a mosaic of secondary vegetation with mature forest fragments, animals dependent on patchy or variable food resources are more vulnerable than those which eat evenly distributed items, since small forest fragments may not include patches of rarer species (Johns, 1985). Many food species important to C. maxwelli are relatively evenly distributed over the forest floor, but larger frugivores dependent on more patchy resources may adapt less well to a mosaic of habitats. Mature forest fragments were included in the ranges of all duikers radio-tracked at Gouleako, although no preference for mature forest over secondary vegetaton was shown.

In secondary vegetation, trees which have reached fruiting age are relatively scarce, but production of foliage is much greater than in mature forest. Folivorous animals are therefore likely to survive best (Marsh and Wilson, 1981; Wilkie, 1987), and some frugivore-folivores can adapt by becoming more folivorous under these conditions (eg. lar gibbon (Hylobates lar) and banded leaf monkey (Presbytis melalophos), Johns, 1983, 1985).

Apart from duikers, three other antelopes and the forest buffalo (Syncerus caffer nanus) are present at Taï. All are folivorous, and therefore do not compete with duikers for food, but observations on their ability to survive in secondary vegetation will be briefly outlined. The royal antelope, Neotragus pygmaeus, (body weight 3 to 4 kg) and the bushbuck, Tragelaphus scriptus (body weight 32 to 77 kg, Jarman, 1974) were both seen only in secondary vegetation, where they were common. The bongo (Boocercus euryceros) (220 kg) was seen by other researchers near the IET station only about four times during the study. It was not reported in secondary vegetation. Villagers agree that bongo populations have decreased considerably since forest exploitation in the seventies, along with the forest elephant (Loxodonta africana cyclotis). Forest buffalo were seen twice, once in secondary vegetation and once on the track leading to the IET station. They were also reported by other researchers in the open vegetation characteristic of inselbergs. Hoppe-Dominik (1989) studied forest buffalo at Taï and found that they were almost exclusively in secondary forest, although they travelled through mature forest in order to reach isolated natural openings and inselbergs. These observations confirm that folivores are more likely to adapt to secondary vegetation than frugivores. The absence of the bongo from secondary vegetation is more likely to be connected to hunting pressures than food availability.

9.2. The ecology of duiker communities at Taï

It is possible from the present study to begin to separate the seven duiker species at Taï according to their ecological rôles.

Table 9.1 summarises our knowledge of each species, and should be compared with Table 1.1 in Chapter 1.

Table 9.1 - Summary of Ecological Characteristics of Cephalophus species found at Taï

SPECIES	BODY WT (kg)[1]	D/N[2]	COMMENTS
C. maxwelli	9	D	Most common species in mature forest and secondary vegetation. Groups of one male with one or two females in 5 - 6 ha home ranges; males territorial. Food items restricted to those under 3 cm diameter or those soft enough to break up before ingestion.
C. zebra	9 - 15	D	Recorded only in mature forest; reported by villagers to raid fields. May live in pairs.
C. niger	15 - 20	D	Second most commonly seen species in secondary vegetation. Also present in mature forest.
C. ogilbyi	14 - 20	D	Recorded only in mature forest; reported by villagers to raid fields.
C. dorsalis	19 - 25	N	Second most commonly seen species in mature forest; also present in secondary vegetation. Polygynous; both sexes territorial.
C. sylvicultor	60 - 80	D+N	In secondary vegetation only.
C. jentinki	70	D+N	Mature forest and Inselbergs only.

[1] Body weights are taken from Wilson (1987), except for C. maxwelli which is taken from the present study.
[2] D = diurnal, N = nocturnal

C. maxwelli, the smallest species, is diurnal and lives in groups of one male with one or two females and their young; only males are territorial. These results are in contrast to previous suggestions that the species is nocturnal (Baudenon, 1958) or active both by day and by night (Aeschlimann, 1963; Ralls, 1973). It was by far the most common species both in mature forest and in secondary vegetation (Chapter 8), and used all habitats studied except open fields and bamboo thickets (Chapter 6). Previous reports suggested that it preferred secondary growth (Aeschlimann, 1963; Baudenon, 1958; Ralls, 1973). It was restricted to dietary items which were either less than 3 cm in diameter, or soft enough to break up before ingestion (Chapter 5). It is likely that the larger duikers are less restricted by size of food items.

C. zebra, the next largest species, had previously been reported as solitary and living in mature forest (Happold, 1973; Kuhn, 1966). It was seen in this study only in mature forest. However, villagers reported that it raided their crops. Of six sightings at the IET site, three were of pairs of adult-sized animals (Chapter 8). Within 5 km of the study site, a pair was seen regularly by other researchers (A. Kurt, personal communication). Two individuals observed at Monrovia zoo were diurnal (Chapter 7).

C. dorsalis, *C. niger* and *C. ogilbyi* all have body weights between 15 and 25 kg (Chapter 1). *C. niger* was present at both sites. It was the most commonly encountered species in secondary vegetation after *C. maxwelli*, which contradicts previous reports that it is found primarily in dense forest (Baudenon, 1958, in Togo; Happold, 1973). Reports by villagers confirmed that it was common in old fields. Five individuals at Monrovia zoo and one animal in an enclosure at Taï were all diurnal, in contrast to reports from a captive study by Dittrich (1972) and from Happold (1973) that the species is nocturnal. C. ogilbyi, for which no previous studies were found, was seen only in mature forest, but was reported by villagers to take crops from fields. Observations of this species were probably artificially low since its colouring is very similar to C. dorsalis and it is often overlooked; however, C. ogilbyi is more similar to C. niger in shape, with a thin mouth and much more slender build than C. dorsalis. One juvenile C. ogilbyi at Monrovia zoo was diurnal.

C. dorsalis is reported in the literature to be polygynous; in Feer's (1988) study of free-living animals, each male had a territory enclosing the territories of two females. It is a heavily built duiker with a thick neck and wide jaws, which may allow the ingestion of larger food items than by similar-sized species. It is nocturnal (Feer, 1988; Hart, 1985; Henle and Apfelbach, 1984; personal observation). Individuals were seen in both mature forest and young secondary vegetation at Gouleako.

The remaining two species, C. sylvicultor and C. jentinki, are separated from all others by their much greater body size (60 to 80 kg; Wilson, 1987). C. sylvicultor was seen only in secondary growth, whereas C. jentinki was reported only in mature forest (including a number of sightings on or near inselbergs), although some previous studies suggest it also raids farmland (Davies and Birkenhager, 1990; Happold, 1973). Thus, there is a clear distinction in habitat use. In some other sites where C. jentinki is absent, C. sylvicultor is present in mature forest (Wilkie, 1987), suggesting a degree of competition. C. jentinki was the only species of duiker which was not reported to be in farmland by villagers; in fact, only experienced hunters were familiar with the species.

The most important factor in niche separation is almost certainly body size. It has been shown that C. maxwelli is restricted in food selection by jaw size; C. zebra may be sufficiently larger to allow selection of larger items. Of the three next largest species, C. dorsalis is separated by its nocturnal habits, and possibly by wider, stronger jaws. C. niger and C. ogilbyi are extremely similar in ecological characteristics - they are of a similar body size and build and both are diurnal. However, C. ogilbyi is more common in mature forest, whereas C. niger lives mainly in secondary vegetation, although both occur in both habitats. It is possible that C. niger is more folivorous than C. ogilbyi, and is thus better able to exploit young vegetation.

A potential competitor with duikers is the water chevrotain, (Hyemoschus aquaticus, Tragulidae), which is a frugivore about the size of the zebra duiker (8 to 13 kg; Happold, 1973). However, it is restricted to riverside vegetation (Dubost, 1978). There were no rivers in the IET study site, but chevrotains were seen by the Audrenisnou river next to the IET station. It was not known whether H. aquaticus was present in secondary vegetation at Gouleako.

These results suggest that four species of duiker adapt well to secondary vegetation, whilst the remaining three are rare or absent outside mature forest. C. sylvicultor and C. niger actively favour secondary vegetation. C. dorsalis was also common there, and estimates of population densities of C. maxwelli suggest it was more abundant in secondary vegetation than in mature forest, in spite of heavier hunting and lower food availability. However, C. jentinki, C. zebra and C. ogilbyi were not recorded in secondary vegetation. Their survival is thus dependent upon the preservation of undisturbed forest. It is perhaps no coincidence that these are the three species regarded as endangered or extremely rare.

9.3 Population dynamics of C. maxwelli and the likely effects of hunting

Populations of C. maxwelli were determined as about 63 km^{-2} in mature, selectively logged forest at IET, and 79 km^{-2} in a mosaic of disturbed habitats at Gouleako (Chapter 8). Information gathered on population structure was limited, mainly by the difficulty of aging and sexing individuals from fleeting glimpses.

During observations, age categories were restricted to infants (under three months old, unweaned and lying up in a hidden 'bed'), juveniles (over three months old, weaned and actively foraging, less than two thirds adult height) and 'adults'. The adult category included some animals which were not yet sexually mature. In addition to the above categories, captured animals with two of the three maxillary molar teeth erupted were designated as M2. The juvenile category probably lasted until an age of about 10 months, and the M2 category from 10 to about 20 months (see Chapters 2 and 7).

Observations at IET (reported in Chapter 7) suggested that adult females were slightly more numerous than adult males (42% and 37% of the total population), while juveniles made up 16%, and infants 5%. Infants were likely to be under-represented in observational data, owing to their immobility. Of 29 animals caught at IET, ten were adult males and ten adult females (34.5% each); five were at the M2 stage (17.2%), and three were juveniles (10.3%) (Appendix 5). Infant animals were generally left undisturbed, and are therefore not included in figures from captures. Bearing in mind that the 'adult' category from observations includes both adults and M2 individuals from captures, the two sets of figures are closely comparable.

These proportions are similar to those of Dubost (1980) on *C. monticola* and Feer (1988, in press) on *C. callipygus* and *C. dorsalis* in lowland rain forest in Gabon. For all three species, the numbers of sexually mature males and females were about equal. In an unhunted population of *C. monticola*, infants and juveniles made up 12% of animals caught by nets, M2 individuals 19%, and older individuals 69%. The latter class consisted of 47% males and 53% females; however, division into subadult animals (20 - 26 months; all milk-teeth replaced) and mature adults showed that in the subadult class, many more females were present, whereas in the adult class, males were slightly more numerous. Females emigrated from the home range at about 18 months (in the M2 stage), whilst males emigrated at about two years (as subadults), and it is likely that the changes in sex ratios reflected the increased mortality rate of each sex at the age of emigration. Similar results were reported for Hyemoschus aquaticus (Dubost, 1978).

Data gathered on C. monticola, from animals caught by hunting with guns or nets and snaring, showed a higher proportion of young animals and a lower proportion of adults. Similarly, Hart and Hart (1989) found higher proportions of subadults in heavily hunted areas than in unhunted areas. 31% of C. callipygus and 40% of C. dorsalis examined by Feer (in press) were M2's. These proportions were far higher than could have been produced by the population of reproductive females, and probably reflect immigration from surrounding areas as territories became vacant due to hunting. The proportion of M2 individuals caught at the IET site in the present study is closer to those described above from unhunted populations. As described below, hunting levels at IET were probably very low.

One M2 female was radio-collared at each study site, and their subsequent history is an indicator of the age of emigration from the parental home range and first reproduction. Gabrielle had presumably already emigrated when first caught in July 1990, since she had no companions and almost no exclusive territory. Robertine was first caught in September 1990 in the company of an adult male, possibly her father, and changed ranges in April to May 1991, when she was between 17 and 27 months old. Thus, of two M2 females, one had emigrated before the first capture and the other emigrated in the subsequent year. It is likely that age of emigration is similar to the other species of Cephalophus described above.

In December 1991, when she would be 27 to 37 months old, Gabrielle was heavily pregnant. Aeschlimann (1963) cites the age at which a female can give birth as 29 months. Thus, the first pregnancy would begin in the subadult stage.

Four of eleven adult females caught were heavily pregnant. However, births were not evenly distributed throughout the year, and data was insufficient to determine the proportion of females reproducing during the birth season. All three of the radio-collared groups at IET produced young early in 1991. The single radio-tagged adult female at Gouleako was lactating when caught in September 1991, so had given birth within the previous three months. These observations, although of a small sample of individuals, suggest that each sexually mature female produced at least one offspring each year. Little is known of infant mortality; at IET, all three groups raised their young successfully to an age of ten months, when the study ended. Dubost (1980) found a mortality rate of 30% during the first year of life, although he cites a figure of 50% as more typical for most artiodactyls.

At IET, only one duiker of the six which were radio-tagged died during the study, following attack by a leopard. The researchers' presence may have deterred poachers from the study site and thus reduced mortality rates. During 1990 shots were heard in and near the study site about twice a month, whereas during 1991 no shots were heard in the immediate area. At Gouleako, mortality was much higher and hunting was far heavier. Three of the four radio-tagged animals were killed by hunters during the study. A 75% level of mortality cannot be sustainable, and populations at Gouleako were almost certainly decreasing very quickly. Nearby villages, such as Ponan, reported that duikers were all but extinct on their land, which had been farmed and hunted more intensively. However, Gouleako has an advantage as a potential site for duiker exploitation since its land is contiguous with the National Park, so immigration by young animals can contribute towards maintaining population densities.

9.4 Implications for management and conservation

The first priority of a management plan for duikers at Taï is the continued preservation of rare or vulnerable species. However, the exploitation of common species for meat has often been put forward as a potentially sustainable system (eg. Wilson, 1987) and would help to provide an infrastructure for monitoring and controlling hunting levels, thus taking pressure off the rarer species. Exploitation could be through farming or through controlled hunting of wild populations. Each of these will be discussed in turn.

The techniques of duiker farming are being studied at Abidjan zoo and will not be discussed here in detail. Instead, we will look briefly at the economic potential of farming. Capital costs include raising the initial animals to breeding age (about 29 months to first parturition for females) and construction of enclosures. Running costs include food, maintenance of fencing, and veterinary bills. At the time of the study, prices of domestic meat in the village of Taï ranged from 1500 CFA ($4.4 USD) / kg for sheep to 800 CFA ($2.6 USD) / kg for rough beef (with bone fragments and gristle). Villagers could not afford these prices, and relied on smoked fish and bushmeat for their daily protein intake. Sheep, goats, pigs and chickens were slaughtered on special occasions. Bushmeat was either obtained by snaring at the edge of farmland, or purchased (illegally) from hunters at prices much lower than those given above.

The mean weight of adult Maxwell's duikers was 9 kg (Appendix 5). Wilson (unpublished) suggests that animals should be harvested at an age of seven months, when growth rates begin to level off and body weight is about 2/3 that of an adult. A 6 kg duiker carcass might produce 3.6 kg of meat. Taking the lowest price of domestic meat (800 CFA / kg), 3.6 kg would be worth 2,880 CFA ($8.5 USD). In order to be economically feasible, the cost of production should be no more than this.

The running costs to produce one animal ready for harvesting can be calculated as BNC + HC, where N is the number of animals kept to produce each offspring (which depends on the number of females which can be kept with a single male); B is the mean interbirth interval; H is the age at which animals are harvested, and C is the cost of keeping one animal for one month (Smythe, 1991). The following figures can be substituted in the equation for Maxwell's duiker:

$N = 1.25$ - one male can be kept with four females (F. N'Golo, personal communication).

B (Mean interbirth interval in captivity) - 8 months (von Ketelholdt, 1977)

H (Age at harvest) - 7 months (body weight about 2/3 adult) (Wilson, unpublished manuscript)

Thus, the cost of producing one animal is

$$BNC + HC = (BN + H)C = 17C$$

Therefore, after capital costs, the cost of keeping one animal for a month would have to be below 2,880/17 CFA = 169 CFA ($0.5 USD). This figure is very low and local pilot schemes are needed to determine its feasibility. Infant duikers are often found during the annual clearance of land for fields (in December to February), and could be reared to establish breeding units, each of one male and four females. A cheap source of fencing must be identified, and an adequate diet determined, based on kitchen scraps and vegetation available near the villages. Expensive mineral blocks are commonly provided for captive duikers to ensure that they retain condition (eg. Farst et al., 1980; F. N'Golo, personal communication; C. Steiner, personal communication), but simple salt-licks may be sufficient (eg. Whittle and Whittle, 1977).

If successful and on a sufficiently large scale, duiker farming could take the pressure of hunting away from wild populations, but contrary to frequent conjecture, would not provide any incentive for the preservation of natural ecosystems. In contrast, a managed hunting programme would encourage the conservation of duiker habitats and tree species important for their diet. It has been shown that four species of duiker survive in mixed forest and farmland such as that around the village of Gouleako. Of these, C. sylvicultor was restricted to secondary vegetation, where it was seen only rarely. It is unsuitable for exploitation, both because of its likely low population density and because in most regions it is regarded as unpalatable. C. niger was common in secondary vegetation and present in mature forest. C. maxwelli and C. dorsalis were both very common. Controlled exploitation of these last three species in secondary growth areas may be possible without damaging populations of the three rarer species in mature forest.

Further research is needed before harvesting levels can be determined. Studies of captive animals are needed to identify reliable methods of determining age, and to investigate growth rates, age at sexual maturity, reproductive cycles and lifespan, and diet. Such studies could be carried out in conjunction with pilot schemes for duiker farming. In addition, more detailed information on duiker population density and structure in secondary vegetation is necessary. At present, the best methods available at Taï are net-catching, supplemented by pellet censuses to determine trends in population size. A study in neighbouring

Liberia, where subsistence hunting outside protected areas is permitted, would allow data to be gathered from carcasses both on population structure and on diets (from stomach contents). Once controlled hunting were permitted in Taï, collection of data from carcasses would allow continuous monitoring of these factors.

The greatest problem envisaged for systems of duiker exploitation concerns the enforcement of hunting laws. At present, hunting is illegal throughout the country, but enforcement is very poor. Hunters kill a wide range of mammalian species, including the rarer duikers and primates. Legalisation of limited hunting would make enforcement still more difficult and could result both in overexploitation of common species, and increased levels of hunting of rare species. Until these problems are addressed, no hunting should be legalised.

Three species of duiker at Taï are regarded as rare, and should not be considered for exploitation. The status and habitat requirements of each of these will be outlined below.

C. jentinki is an endangered species and in 1991 was placed on Appendix 1 by CITES. It was rare at Taï. It is unlikely that this was due wholly to a naturally low population density connected to large body size, since in the neighbouring forest in Liberia, it was reported to be one of the most common species (H. Gilmore, personal communication). It is likely that C. jentinki has suffered from hunting pressure in the past, along with other large terrestrial mammals such as the forest elephant and the bongo. The species almost certainly needs mature forest and therefore the numbers in Côte d'Ivoire outside the Taï National Park are likely to be negligible. Its distribution is limited to Sierra Leone, Liberia and the Western part of Côte d'Ivoire, so Taï is its only large protected refuge.

C. zebra, which has the same distribution as *C. jentinki*, and *C. ogilbyi*, which is found throughout West Africa, are also thought to be rare. Although villagers indicated that both were present in secondary vegetation, this was not confirmed, and they may be reliant on mature forest. However, *C. ogilbyi* was the third most frequently seen species in mature forest. Its presence is often overlooked as it is mistaken for *C. dorsalis*, and the author's feeling was that it is not uncommon in the forest at Taï. Villagers were familiar with the species and five were killed by hunters during the short time that hunting was monitored in a local village.

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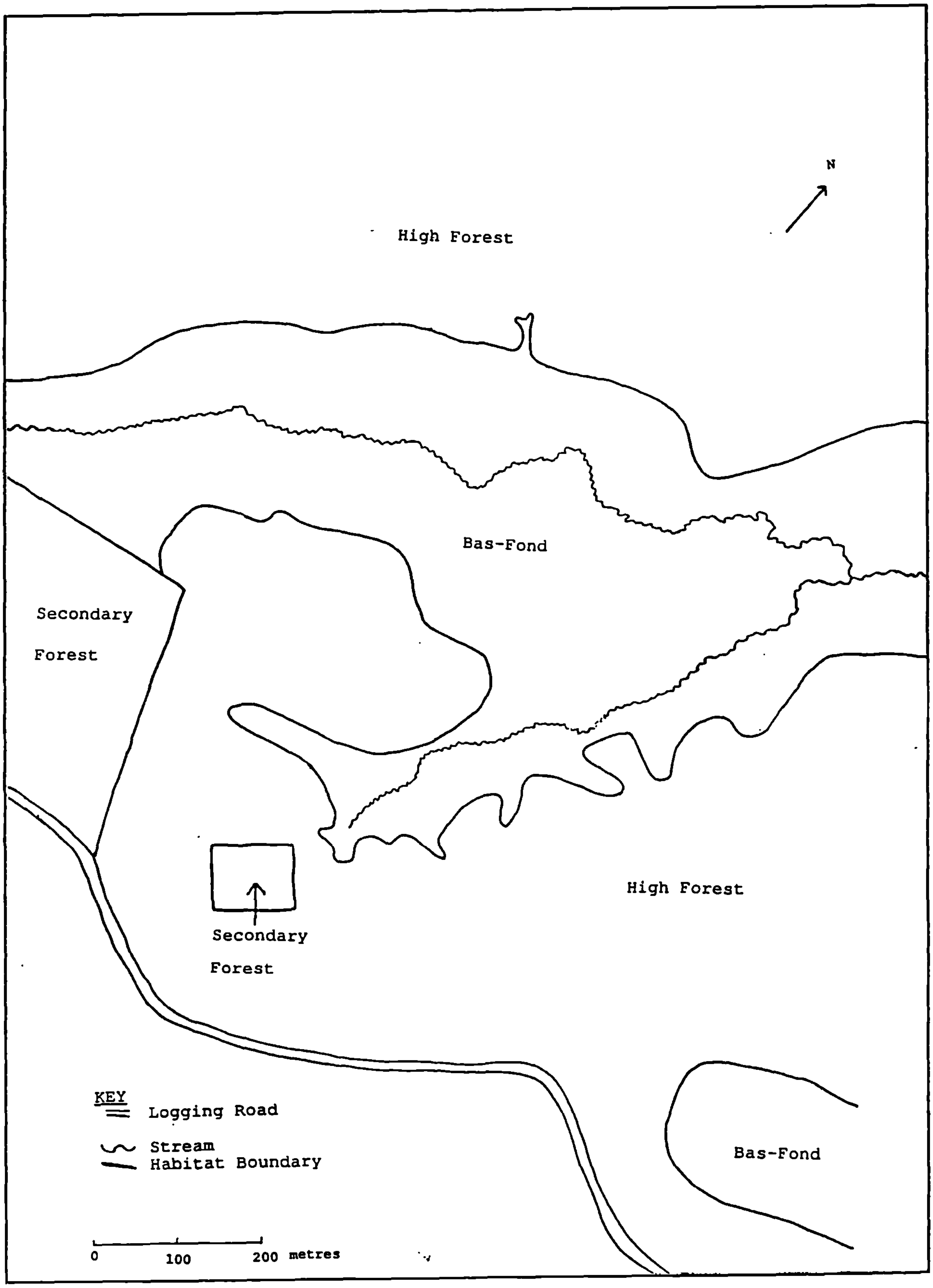
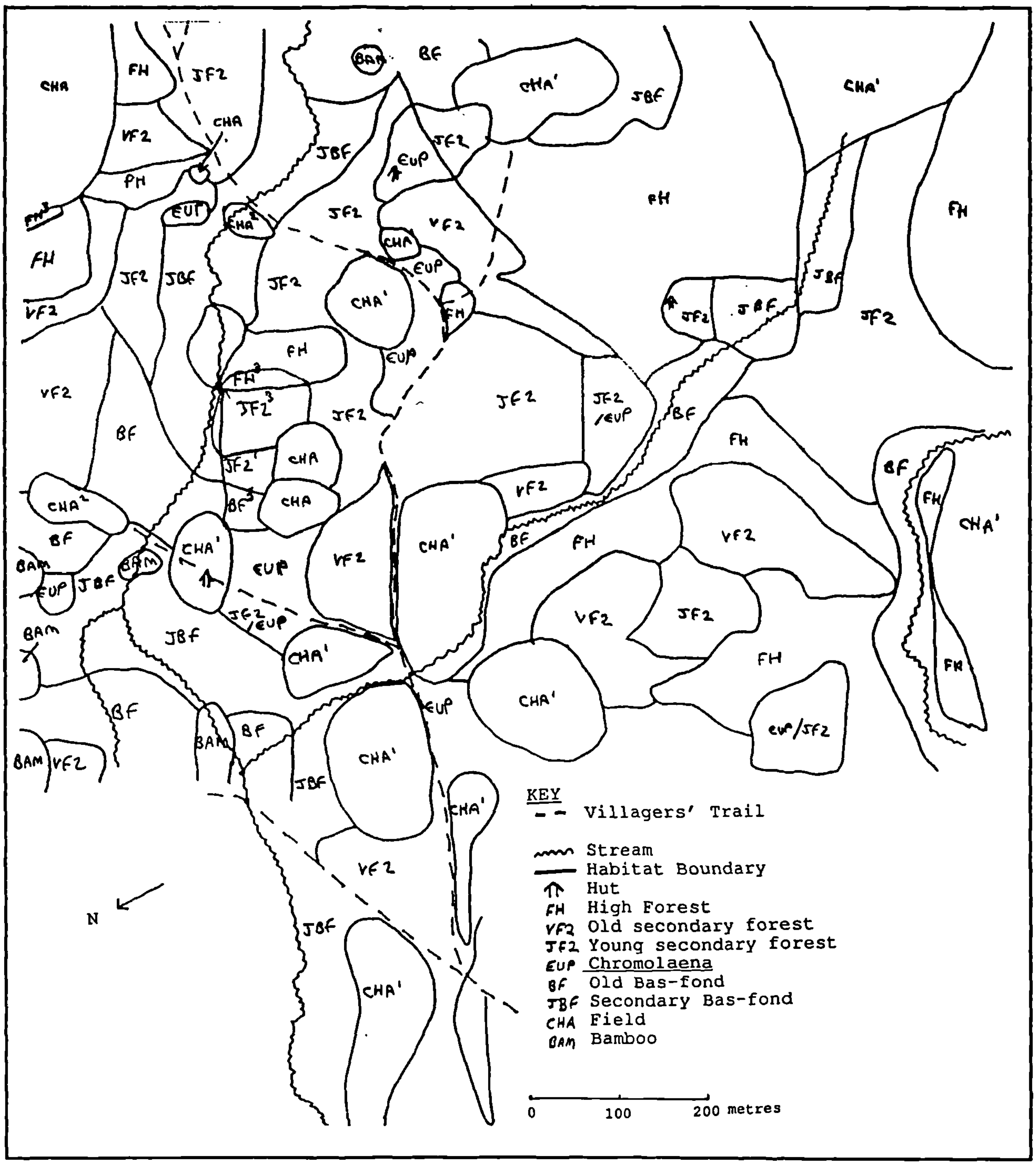
Appendix 1

a) IET study site



Appendix 1
b) Gouleako study site



<u>Note</u>: Footnotes shows following vegetation changes by May 1991, as follows:
[1] To <u>Chromolaena</u> thicket; [2] To young bas-fond; [3] To fields.

Appendix 2 List of mammals recorded in Taï National Park
(Adapted from Roth and Merz (1986))

Species	Common Name	Source[1]
INSECTIVORA		
Soricidae	**Shrews**	
Sylvisorex megalura		2
Crocidura bottegi		2
C. buettikoferi		2
C. crossei		2
C. dolichura		2
C. douceti		2
C. flavescens		2
C. grandipes		2
C. lamottei		2
C. odorata		2
C. poensis		2
C. theresae		2
C. wimmeri		2
C. occidentalis		2
CHIROPTERA	**Bats**	
Pteropodidae		
Epomops buettikoferi		2
E. franqueti		2
Myonycteris torquata		2
Hypsignathus monstrosus		2
Epomorphorus gambianus		2
Scotonycteris ophidion		2
S. zenkeri		2
Nanonycteris veldkampi		2
Eidolon helvum		2
Megaloglossus woermanni		2

Species	Common Name	Source[1]
Rousettus aegyptiacus unicolor		2
R. angolensis smithi		2
Emballonuridae		
Taphozous peli		2
T. mauritianus		2
Nycteridae		
Nycteris grandis		2
N. macrotis macrotis		2
N. hispida hispida		2
N. arge		2
N. nana		2
Rhinolophidae		
Rhinolophus landeri		2
R. alcyone		2
R. fumigatus		2
R. denti		2
R. maclaudi		2
Hipposideridae		
Hipposideros jonesi		2
H. cyclops		2
H. abae		2
H. ruber guineensis		2
H. beatus beatus		2
H. commersoni gigas		2
H. marisae		2
Verspertilionidae		
Eptesicus tenuipinnis		2
E. brunnens		2
E. pusillus		2
Mimetillus moloneyi moloneyi		2
Glauconycteris poensis		2

Species	Common Name	Source[1]
G. superba		2
Myotis bocagei cupreolus		2
Pipistrellus nanus		2
Miniopterus schreibersi		2
Kerivoula muscilla		2
K. phalaena		2
Molossidae		
Tadarida nanula		2
T. thersites		2
T. leonis		2
T. condylura		2
T. pumila		2
Xiphonycteris spurrelli		2
Myopterus whitheyi		2
PRIMATES	**Primates**	
Lorisidae		
Perodicticus potto	Potto	1,2
Galago demidovii	Demidoff's galago	1,2
Cercopithecidae		
Cercopithecus mona lowei	Mona monkey	1,2
C. diana diana	Diana monkey	1,2
C. petaurista	Lesser spot-nosed monkey	1,2
C. nictitans	Greater spot-nosed monkey	1,2
Cercocebus torquatus atys	Collared mangabey	1,2
Colobus verus	Olive colobus	1,2
C. badius badius	Red colobus	1,2
C. polykomos polykomos	Black and white colobus	1,2
Pongidae		
Pan troglodytes verus	Chimpanzee	1,2

Species	Common Name	Source[1]
PHOLIDOTA		
Manidae	**Pangolins**	1,2
Manis gigantea	Giant pangolin	1,2
M. tricuspis tricuspis	White-bellied pangolin	1,2
M. tetradactyla	Long-tailed pangolin	1,2
RODENTIA	**RODENTS**	
Anomaluridae	**Flying squirrels**	
Anomalurus derbianus	Lord Derby's flying squirrel	1,2
A. peli	Pel's flying squirrel	1,2
A. beecrofti	Beecroft's flying squirrel	2
A. pusillus	Little flying squirrel	Gartshore (1989)
Idiurus macrotis		2
Thryonomidae		
Thryonomys swinderianus		1,2
Sciuridae	**Squirrels**	
Xerus erythropus		2
Protoxerus stangeri temminckii	Giant squirrel	1,2
P. aubinnii		2
Heliosciurus rufobrachium		2
Epixerus ebii jonesii		1,2
Paraxerus poensis		2
Funisciurus pyrrhopus leonis		1,2
F. substriatus		2
Hystricidae	**Porcupines**	
Atherurus africanus		1,2
Hystrix cristata		1,2

Species	Common Name	Source[1]
Cricetidae		
Cricetomys emini		2
C. gambianus	Gambian rat	1,2
Gliridae		
Graphiurus hueti		2
G. murinus		2
G. crassicaudatus		2
Muridae		
Hybomys trivirgatus planifrons		2
H. univittatus		2
Praomys baeri		2
P. aeta		2
P. simus		2
P. tullbergi		2
P. erythroleucus		2
P. ingoldbyi		2
Mus minutoides musculoides		2
M. setulosus		2
Malacomys edwardsii		2
M. longipes		2
Lophuromys sikapusi		2
Stochomys defua		2
Thamnomys rutilans		2
Dasymys incomtus		2
Lemniscomys striatus		2
Mastomys huberti		2
Mylomys dybowskyi		2
Oenomys hypoxanthus		2
Rattus rattus		2
CARNIVORA	**Carnivores**	

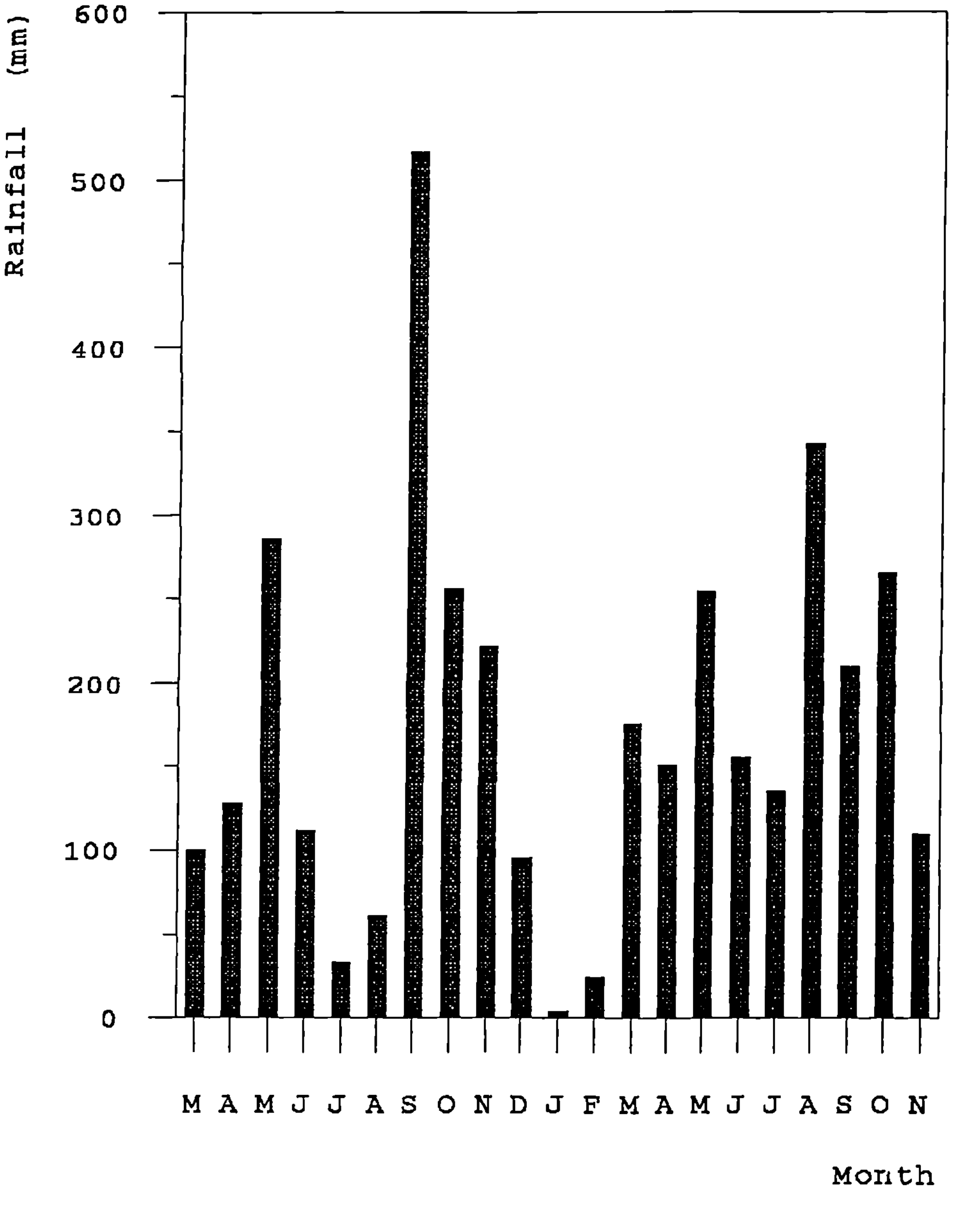
Species	Common Name	Source[1]
Mustelidae		
Mellivora capensis cottoni	Ratel	1,2
Lutra maculicollis maculicollis	spot-necked otter	1,2
Aonyx capensis capensis	Cape clawless otter	1,2
Viverridae		
Atilax paludinosus pluto	Marsh mongoose	1,2
Crossarchus obscurus	Cusimanse	1,2
Liberiictus kuhnii	Liberian mongoose	2, Gartshore
Viverra civetta civetta	African civet	1,2
Nandinia binotata binotata	2-spotted palm civet	1,2
Genetta tigrina	Rusty-spotted genet	
G. pardina	Pardine genet	1,2
G. johnstonii	Johnstone's genet	
Poiana richardsoni liberiensis	African linsang	1,2
Herpestes ichneumon	Ichneumon mongoose	(1)
H. sanguineus	Red mongoose	(1)
Felidae	**Cats**	
Felis aurata celidogaster	Golden cat	1,2
Panthera pardus leopardus	Leopard	1,2
PROBOSCIDEA		
Elephantidae		
Loxodonta africana cyclotis	Forest elephant	1,2
HYRACOIDEA		
Procaviidae		
Dendrohyrax arboreus	Tree hyrax	1,2
SIRENIA		

Species	Common Name	Source[1]
Trichecus senegalensis	African manatee	(1)
ARTIODACTYLA		
Suidae	**Pigs**	
Hylochoerus meinertzhageni ivoriensis	Giant forest hog	1,2
Potamochoerus porcus porcus	Bushpig	1,2
Hippopotamidae	**Hippos**	
Choeropsis liberiensis liberiensis	Pygmy hippo	1,2
Tragulidae		
Hyemoschus aquaticus	Chevrotain	1,2
Bovidae		
Cephalophus maxwelli	Maxwell's duiker	1,2
Cephalophus niger	Black duiker	1,2
C. dorsalis	Bay duiker	1,2
C. zebra	Zebra duiker	1,2
C. ogilbyi	Ogilby's duiker	1,2
C. jentinki	Jentink's duiker	1,2
C. sylvicultor	Yellow-backed duiker	1,2
Neotragus pygmaeus	Royal antelope	1,2
Tragelaphus scriptus scriptus	Bushbuck	1,2
Boocercus euryceros	Bongo	1,2
Syncerus caffer nanus	Forest buffalo	1,2
Limnotragus spekei gratus	Sitatunga	(1)

[1] Reported by Roth and Merz (1986) from literature, but presence in doubt.

Appendix 3

Monthly Rainfall, March 1990 - Nov 1991 Tai National Park



Appendix 4 Report on the capture of Maxwell's duiker in and around Taï National Park, Côte d'Ivoire

Summary

Four methods to capture Maxwell's duikers (Cephalophus maxwelli) were evaluated as part of a study of their ecology in a variety of habitats in the Taï region of Côte d'Ivoire, West Africa. Between May 1990 and December 1991, 41 captures were made, 35 in climax forest in Taï National Park and 6 in fallow farmland outside the Park (See Appendix 3). Each animal was weighed, measured, examined and marked with a tattoo. Twelve were fitted with radio-collars. Blood and faecal samples were taken from those caught in 1991. They were then re-released at the place of capture. Of the methods used, the most effective in the forest was capture with nets at night, developed during this project. In fallow farmland the dense undergrowth made this method impossible, and the method of daytime drives was used.

Introduction

The standard method of catching small forest ungulates involves setting up nets around one hectare blocks of forest and chasing animals into the nets (eg. Harding, 1986; Feer, 1988). This was the first method to be tried, but it proved both labour-intensive and time-wasting. Three other methods were also tried, which were based on traditional hunting techniques used throughout West Africa. Firstly, a modified snare system was used; secondly, duikers were attracted by calls used by hunters; and thirdly, duikers were sought by torchlight at night and encircled with nets. Each of the four techniques which were tried is described in detail below, and results are given in terms of success rates and apparent effects of capture on the duikers. In conclusion, the advantages and disadvantages of each method are briefly discussed.

Methods

1. Daytime net-capture Following the standard method, one-hectare blocks were enclosed by eight 55 m long, 1.5 m high black nylon nets with a 2.5 cm diamond mesh. A minimum of twelve people were involved to set the nets up along pre-cut transects, and they worked in four teams, one on each side of the block. The nets were attached to trees at the top by nylon cords and were pegged to the ground every one or two metres with wooden pegs. Logs were used to block holes around obstructions such as fallen trees. It proved important to take great care setting the nets up firmly and blocking all gaps - until the team became accustomed to doing this a number of duikers escaped by pushing under the nets or jumping over them.

It took about 45 minutes to erect the nets. Once they were in place, eight people were placed near the nets around half the hectare to guard for duikers, and four or more people searched through the area in a line at a walking-pace, making much noise and paying special attention to thickets and treefalls. If no duikers were found, the second half of the hectare was searched in the same way. When a duiker was flushed it was chased and would eventually run into a net where it could be captured. Duikers nearly always broke back through the line of searchers and would sometimes run back and forth for some minutes before running into a net, so it was essential that all four sides of the hectare were netted securely. When an animal was caught, it was put in a sack and hung from a tree, where it would stay quietly until we were ready to work with it.

In climax forest, where undergrowth is relatively sparse, each hectare took a total of 1.5 to 2 hours . In a full day, six hectares could be searched in this way. In thick secondary vegetation, however, it was not possible to chase through the undergrowth at speed and the above method had to be slightly modified. A hectare was enclosed with nets as usual, but then extra transects were cut to divide it into four parts and each quarter was searched separately. If a duiker was seen it usually ran into another quarter of the hectare, and the nets were moved to enclose it in a smaller area. Eventually it would be enclosed in an area 50 m x 50 m, when it was possible to chase it into a net and catch it. However, each hectare took 3 or 4 hours by this method.

2. Snaring With the help of local villagers, modified snares were constructed on clearly visible animal trails in the forest. Ten to twelve snares could be constructed in a day. A thick, soft nylon cord was attached to a small sapling which was bent over to act as a spring; the other end of the cord was attached to a piece of wood which acted as a trigger, set over a small hole in the ground covered with twigs. When an animal trod on the hole the twigs collapsed, releasing the trigger, and the cord tightened around the animal's leg. To minimise the risk of injury to the animals caught, each snare was tested by springing it with a hand to make sure the tension was not too great.

In addition to setting snares on animal trails, various methods were tried to identify places which were frequented regularly by duikers, and also to attract duikers to a particular place so as to increase the likelihood of a nearby snare being sprung. Fruiting trees were observed from hidden positions for full days to see whether duikers came at regular times. A salt-lick was established and maintained for two months, during which visits by animals were monitored every few days by noting footprints. A patch of cultivated fruits such as bananas, oranges and pineapples was established by a stream where duiker tracks were plentiful, and monitored.

The snares were checked day and night every two to four hours - some by visits, others remotely by radio transmitters set to begin transmitting when the trap was sprung.

3. Duiker calls A villager skilled in calling duikers was taken into the forest by the author by day and by night to make a traditional nasal call which is said to attract duikers. Calls were made at least 400 m apart. Before each call the caller and the author hid behind a log or at the foot of a buttress tree. Once the efficacy of the calling had been tested in this way, attempts were made to catch duikers which approached, either by throwing nets over them or by hiding a number of people nearby to drive the animals into nets which were set up one or more days previously.

4. Night-time net-capture Seven people walked transects at night between 2100 hours and 0500 hours. Two people walked 20 - 30 m ahead of the rest and searched for duikers in the manner used by hunters, with strong torches strapped to their heads. These two people changed with others once or twice during a night's search, so that concentration could be kept high. Duiker eyes reflect yellow or orange in torchlight. When a duiker was found, it was dazzled with a very strong torch (Mag-lite 5 D-cell). If it stayed still, the rest of the team then approached, and while one person kept the torch on the duiker's eyes, the other six worked in pairs to encircle it with three nets at a distance of 5-15 m. The nets were attached as described above for day-time net captures. Once the nets were up, three people approached the duiker while four stayed at the nets to catch it as it ran.

Treatment of Captured Duikers

The data noted for each animal caught are given in Chapter 2 and an example of a datasheet is given as Appendix 3. Every effort was made to minimise stress to the animals caught - catchers not helping to handle them stayed at a distance and noise was kept to a minimum. All animals were released at the place of capture within 20 minutes of capture, and were watched on release until they ran out of sight.

Results

Success rates

1. Day-time net-capture In climax forest, 48 hectares were searched by this method in the test period. A total of eleven duikers were seen, in seven hectares. The species seen were as follows:-

6 C. maxwelli

1 C. ogilbyi

2 C. dorsalis

2 C. spp. (unidentified).

The average encounter rate dropped from one hectare in four to one in six after the first 12 drives, then stayed constant. Only C. maxwelli were seen during the later drives (after drive 12), so it is possible that the other species learned to avoid the drives. They were still present in the study area and were occasionally seen during other types of work. Once, two C. maxwelli were seen leaving a hectare block as nets were erected around it. At the end of the study when radio-tagged duikers were located and recaptured for removal of their collars, it was possible to monitor their movements as the capture team approached. Most of them showed no response to our approach, but one, which had been the most timid during the whole study, repeatedly fled long before we were in sight of her. Twice, she fled right out of the study area and returned some hours later. She reacted similarly to approaches at night. It is therefore probable that encounter rates of duikers during catches are artificially low. This finding has important implications for studies in which duiker drives have been used to estimate duiker population densities. However, the success rate of capture of duikers encountered increased as expertise in making the nets secure improved.

In secondary vegetation, eleven hectares were searched. Three of them contained duikers - each one a male-female pair of C. maxwelli. Five of the six duikers seen were caught.

2. Snaring In a total of 195 snare-days, snares were sprung eight times. Only one genet and one duiker were caught. The latter was an infant Maxwell's duiker (body weight 3.25 kg). In spite of efforts to ensure that the snares would not harm duikers, the snare had caused some bruising on the infant's leg and when released it was limping; as a result of this and the poor success rate, snaring was discontinued[1].

Observations of duikers at fruiting trees were not frequent enough to merit setting up additional snares nearby, especially as the duikers observed used a slightly different path each time as they foraged over a fruit-patch. The attempts to attract duikers by salt-licks and artificial fruit-patches were not successful.

3. Duiker calls By day, three of nine calls produced a response. Two times a Maxwell's duiker approached, and once a bay duiker (C. dorsalis). All came within 3 metres of the caller and hesitated for at least 30 seconds before running

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[1] The same animal was caught again some months later and had completely recovered from this incident.

off. At night, two of six calls attracted duikers (one Maxwell's and one bay). However, the animals were too wary for it to be possible to throw nets over them. When there were nets and additional people hidden nearby, only once did a duiker come to a call (of numerous attempts in 6 locations), and it became nervous and bolted before it was inside the line of chasers.

4. Night-time net capture In climax forest, 11.8 km were walked in six nights during the test period, taking a total of 20 hours 15 minutes. Twenty two duikers were seen in fourteen encounters, as follows:-

16 C. maxwelli

2 C. dorsalis

2 C. spp. (unidentified).

Although the mean number of duikers encountered per kilometre walked did not vary greatly between nights, the number of successful captures did vary. During three consecutive nights in July, three duikers were caught; during two consecutive nights in August, nothing was caught and the duikers seen were visibly nervous, moving quickly away from the torchlight; in a single night in September, two animals were caught and a third was successfully surrounded by nets but climbed over them and escaped. There was more moonlight during the August hunts, which may have contributed to the duikers' increased nervousness; also, on one of these nights, a leopard was calling close by throughout the hunt. Further night catches were limited to the two weeks of the month when the moonlight is least strong. In February 1991, eight duikers were caught in nine nights, and in November and December 1991, thirteen duikers were caught in seven nights.

In secondary growth, a total of 8 km was walked over two consecutive nights in September 1990, taking a total of seven hours. Only three duikers were seen (species not determined). Visibility was very poor because of the dense vegetation, and it was not possible to erect nets off the transects to trap the duikers which were seen.

Effects of Capture on the Duikers

Netting On capture, Maxwell's duikers bleated continuously and appeared to be stressed, but on re-release all except two trotted off immediately showing no signs of injury or prolonged trauma. Radio-monitoring showed that they quickly settled back into their normal pattern of activity. Some animals seemed noticeably wary of people for the first few days after capture, showing exaggerated alarm responses, but this effect disappeared within a few days in all but one individual.

Two male C. maxwelli did show distress after release and tried repeatedly to remove the radio-collars with their hind legs. The collars were checked and re-adjusted if necessary, but the animals continued to react badly. The first time this happened, the animal was left alone to recover, but two days later it was dead. The second time, the animal was observed for 15 minutes and as there was no sign of improvement the collar was removed. When this was done the duiker immediately ran off, with no sign of injury.

Thus no ill effects of net capture were observed, but two individuals reacted strongly against the radio-collars, and one died as a result. It is essential to monitor animals for a short while on release in order to identify those which will not adapt to carrying a collar.

Snaring As mentioned above, the one duiker caught was slightly injured on the leg, which was one reason why snaring was discontinued.

Discussion: Evaluation of Methods

1. Daytime net capture

This method has been used most often in previous studies of forest ungulates. However, it is very labour-intensive and in the climax forest encounter rates with duikers were low. If an animals is at a known location this method works well - for example it was used to catch duikers accompanying those with radio-collars, by erecting the nets around the hectare known to contain the collared animal.

In secondary growth encounter rates were higher, perhaps because in the thick undergrowth, duikers are more likely to hide when they hear people approaching, rather than to move away. This may explain why the method had poorer encounter rates in the climax forest than in previous studies elsewhere, as the Taï forest has relatively sparse undergrowth compared to other forests where duikers have been studied (eg. Makokou, Gabon; F. Feer, personal communication).

2. Snares

It should be possible to develop a snare which is harmless to the animals which are caught, but at present the risk of injury is higher by this method than by the other methods discussed. Setting up snares and monitoring them is time-consuming and gives a poor rate of return, even when done by villagers experienced in catching duikers by this method. In addition, snares are not duiker-specific and other species of animal may be caught, which is unnecessarily disruptive to the animals and could be dangerous to the researchers.

3. Duiker calls

Duiker calls worked well to attract animals, but a successful means of capture was not found. Animals called in could easily be darted with tranquilisers, but the drugs commonly used take approximately 8 minutes to work, so radio-tags would be needed on the darts to find the drugged animals. In addition, dosages needed are likely to vary greatly. Since Maxwell's duikers are easy to handle without anaesthetics, it is preferable not to use them.

4. Night-time net capture

This method gave the best results in climax forest, as long as well-cleared transects were used so that noise was kept to a minimum and concentration on searching for duikers was not broken by having to search for the path. In thick vegetation such as young secondary growth, this method could not be used because visibility was poor and because it was not possible to put up the nets off the transects without cutting back the vegetation.

Conclusion

The night-time net capture method was most efficient in climax forest where undergrowth is relatively sparse. In dense secondary growth the daytime net capture method was the only method which was successful. Snaring has a low rate of success and has some risk of injury. Hunting calls work well in attracting duikers but no method was found by which animals called in could be caught.

References

Feer, F. (1988), Strategies ecologiques de deux especes de Bovides sympatriques de la foret sempervirente africaine (*Cephalophus callipygus* et *C. dorsalis*): Influence du rythme d'activite. Dsc., Universite Pierre et Marie Curie, Paris.

Harding, S. (1986), Aspects of the Ecology and Social Organisation of the muntjac deer *Muntiacus reevesi*. PhD Thesis, Oxford.

Appendix 5

Details of duikers caught during the study

Site	Date	Sex	Age	Name of radio-collared animals; comments	Weight (kg)
C. maxwelli:					
IET	30/5/90	♂	A	Mae Mae	10.3
	27/6/90	♀	A	Christiane	9.8
	26/4/90	♂	I	1st molar erupted	3.3
	12/7/90	♂	A		9.5
	12/7/90	♀	A	Germaine (Pregnant)	11.0
	12/7/90	♀	M2	Gabrielle. 2nd molar erupted.	8.5
	18/10/90	♂	A	Lucien	9.8
	16/10/90	♂	A	Lucbersone	8.0
	11/2/91	♀	A		10.0
	11/2/91	♀	J	1st molar erupted	5.0
	11/2/91	♂	M2	2nd molar erupted	7.0
	11/2/91	♂	A		11.0
	13/2/91	♀	A		9.0
	14/2/91	♀	A	Pregnant	11.0
	20/2/91	♀	A	Pregnant	12.5
	20/2/91	♀	A		8.0
	26/11/91	♀	M2	2nd molar erupted	6.8
	26/11/91	♂	M2	2nd molar erupted	6.5
	27/11/91	♂	A		9.0
	27/11/91	♀	A		9.8
	28/11/91	♂	M2	2nd molar erupted	5.8
	03/12/91	♂	A	Mae Mae	8.6
	04/12/91	♂	A		9.0
	04/12/91	♀	A		7.8
	05/12/91	♀	J	1st molar erupted	4.8
	05/12/91	♂	A		9.4

Appendix 5

Details of duikers caught during the study

Site	Date	Sex	Age	Name of radio-collared animals; comments	Weight (kg)
	05/12/91	♂	A		8.2
	10/12/91	♀	J	With Christiane; 10 months old. 2nd molar half erupted.	7.5
	10/12/91	♀	A	Christiane	10.0
	11/12/91	♂	A	Lucien	8.5
	12/12/91	♂	A	Lucbersone	9.0
	12/12/91	♀	A	Gabrielle (pregnant)	9.5
	12/12/91	♂	A	With Gabrielle	8.0
GOU	27/9/90	♂	A	Père Abraham	8.0
	27/9/90	♀	M2	Robertine. Second molar erupted.	8.0
	03/10/90	♀	A	Aline	11.0
	04/10/90	♂	A	Luis	8.0
	06/2/91	♂	A		8.5
	17/9/91	♂	A		-
	17/9/91	♀	A	Aline (Lactating)	-
<u>C. dorsalis</u>:					
IET	27/11/91	♀	J	1st molar erupted	12.5
	02/11/91	♂	A		15.5

KEY:

Sex: ♂ = Male, ♀ = Female
Age: A = Adult, J = Juvenile, I = Infant, M2 = juvenile with second molar erupted

Note: Mean body weight of all adults excluding pregnant females was 9.1 kg. (Males 9.1 kg, females 9.2 kg)

Appendix 6 List of plant species recorded

	Growth form[1]
Acanthaceae	
Asystasia vogeliana Benth.	s
Brillantaisia lamium (Nees) Benth.	h
Crossandra flava Hook	h
Crossandra sp.	h
Elytraria maritima J. K. Morton	h
Mendoncia combretoides (A. Chev.) Benoist.	l
Physacanthus nematosiphon (Lindau) Rendle & Britten	h
Pseuderanthemum tunicatum (Afzel.) Milne-Redhead	h
Staurogyne paludosa (Mangenot & Aké Assi)	h
Thunbergia togoensis Lindau	l
Whitfieldia colorata C. B. Cl. ex Stapf	s
Adiantaceae	
Pityrogramma calomelanos (Linn.) Link	h
Pteris atrovirens Willd.	h
Pteris burtoni Bak.	h
Agavaceae	
Dracaena elliotii Bak.	h
Dracaena humilis Bak.	h
Dracaena ovata Ker-Gawl.	h
Dracaena surculosa Lindl.	h
Amaranthaceae	
Cyathula prostrata (Linn.) Blume	h
Anacardiaceae	
Lannea welwitschii (Hiern) Engl.	a
Pseudospondias microcarpa (A. Ric) Engl.	a
Tricoscypha arborea (A. Chev.)	a
Tricoscypha bequei (Aubrev.& Pellegr.)	a
Tricoscypha oba (Aubrev. & Pellegr.)	a
Annonaceae	
Cleistopholis patens (Benth.) Engl. & Diels	a
Enantia polycarpa Engl. & Diels	a
Monodora myristica (Gaertn.) Dunal	a
Monodora tenuifolia Benth.	a
Neostenanthera gabonensis (Engl. & Diels) Exell	s
Pachypodanthium staudtii Engl. & Diels	a
Polyalthia oliveri Engl.	a
Polyceratocarpus parviflorus (Bak. f.) Ghesq.	a
Popowia mangenotii Sillans	l
Popowia whytei Stapf	s
Uvaria afzelii Sc. Elliot	a
Uvaria baumannii Engl. & Diels	l
Uvariastrum insculptum (Engl. & Diels) Sprague & Hutch.	s
Uvariodendron mirabile	a
Uvariodendron sp.	a
Uvariopsis guineensis Keay	a
Uvariopsis sp.	a

Xylopia aethiopica (Dunal) A. Rich.	a
Xylopia parviflora (A. Rich.) Benth.	a
Xylopia quintasii Engl. & Diels	a
Xylopia taiense	a
Xylopia villosa Chipp	a
Apocynaceae	
Aphanostylis leptantha (K. Schum.) Pierre	s
Aphanostylis mannii (Stapf) Pierre	s
Baissea breviloba Stapf	s
Baissea leonensis Benth.	s
Baissea zygodioides (K. Schum.) Stapf	l
Funtumia elastica (Preuss) Stapf	a
Hunteria eburnea Pichon	a
Landolphia dulcis (R. Br. ex Sabine) Pichon	l
Landolphia hirsuta (Hua) Pichon	l
Landolphia membranacea (Stapf) Pichon	l
Landolphia owariensis P. Beauv.	l
Oncinotis gracilis Stapf	s
Picralima nitida (Stapf) Th. & H. Dur.	a
Rauvolfia vomitoria Afzel.	s
Strophanthus sarmentosus DC.	l
Araceae	
Anchomanes difformis Engl.	h
Anubias gigantea A. Chev.	l
Anubias gracilis A. Chev.	l
Anubias sp.	
Cercestis afzelii Schott	l
Colocasia esculenta (L.)	h
Culcasia mannii (Hook. f.) Engl.	h
Culcasia parviflora N. E. Br.	h
Culcasia saxatilis A. Chev.	h
Culcasia scandens P. Beauv.	h
Culcasia striolata Engl.	l
Nephthytis afzelii Schott	h
Rhaphidophora africana N. E. Br.	l
Asclepiadaceae	
Parquetina nigrescens (Afzel.) Bullock	l
Pergularia daemia (Forsk.) Chiov.	l
Secamone afzelii (Schultes) K. Schum.	s
Mondia whitei (Hook. f.) Skoels	l
Aspleniaceae	
Asplenium africanum Desv.	h
Asplenium sp.	h
Asplenium variabile Hook.	h
Bolbitis auriculata (Lam.) Alston	h
Bolbitis gaboonensis (Hook.) Alston	h
Bolbitis sp.1	h
Bolbitis sp. 2	h
Ctenitis pilosissima (J. Sm.) Alst.	h
Ctenitis vogelei (Hook.) Ching	h
Lomariopsis sp.	h
Lomariopsis guineensis (Underw.) Alston	h

Bignoniaceae	
Stereospermum sp.	a
Bombacaceae	
Ceiba pentandra (Linn.) Gaertn.	a
Bromeliaceae	
Ananas comosus (L.)	h
Burseraceae	
Canarium schweinfurthii Engl.	a
Dacryodes klaineana (Pierre) H. J. Lam.	a
Caesalpiniaceae	
Afzelia bella Harms	s
Amphimas pterocarpoides Harms	a
Anthonotha crassifolia J. Léonard	a
Anthonotha fragrans (Bak. F.) Exell & Hillcoat	a
Anthonotha macrophylla P. Beauv.	a
Cassia aubrevillei Pellegr.	a
Chidlowia sanguinea Hoyle	a
Dialium aubrevillei Pellegr.	a
Dialium dinklagei Harms	a
Distemonanthus benthiamanus Baill.	a
Erythrophleum ivorense A. Chev.	a
Gilbertiodendron limba (Sc. Elliot) J. Léonard	a
Gilbertiodendron splendidum (A. Chev. ex Hutch. & Dalz.) J. Léonard	a
Griffonia simplicifolia (Vahl ex DC) Baill.	s
Griffonia sp.	l
Guibourtia ehie (A. Chev.) J. Léonard	a
Hymenostegia afzelii (Oliv.) Harms	a
Mezonevron benthamianum Baill.	l
Plagiosiphon emarginatus (Hutch. & Dalz.) J Léonard	a
Capparidaceae	
Euadenia eminens Hook. f.	s
Euadenia trifoliolata (Schumm. & Thonn.)	s
Cecropiaceae	
Musanga cecropioides R. Br.	a
Myrianthus arboreus P. Beauv.	a
Myrianthus libericus Rendle	a
Celastraceae	
Cuervea macrophylla (Vahl) R. Wilcz. ex N. Hallé	l
Loeseneriella rowlandii (Loes.) N. Hallé	l
Salacia calumna N. Hallé	l
Salacia debilis (G. Don) Walp.	l
Salacia erecta (G. Don) Walp.	s
Salacia leonensis Hutch. & M. B. Moss	s
Salacia nitida (Benth.) N. E. Br.	l
Salacia sp.	l
Salacia zenkeri Loes	l
Chrysobalanaceae	

Hirtella butayei (De Wild.) Brenan		a
Licania elaeosperma (Mildbr.) G. T. Prance & F. White		a
Parinari aubrevillei Pellegr.		a
Parinari excelsa Sabine		a
Parinari glabra Oliv.		a
Combretaceae		
Combretum hispidum Laws		s
Combretum homalioides Hutch. & Dalz.		l
Combretum platypterum (Welw.) Hutch. & Dalz.		s
Combretum racemosum P. Beauv.		s
Combretum sp.		l
Strephonema pseudocola A. Chev.		a
Terminalia ivorensis A. Chev.		a
Terminalia superba Engl. & Diels		a
Commelinaceae		
Aneilema beninense Kunth.		h
Aneilema umbrosum Kunth.		h
Buforrestia mannii C. B. Cl.		h
Commelina diffusa Burm. f.		h
Commelina lagosensis C. B. Clarke		h
Commelina sp.		h
Floscopa africana C. B. Clarke		h
Palisota sp.	h	
Palisota barteri Hook.		h
Palisota hirsuta K. Schum.		h
Compositae		
Adenostemma perrottetii DC		h
Ageratum conyzoides Linn.		h
Erigeron floribundus (H. B. & K.) Sch. Bip.		h
Chromolaena odorata ex *Eupatorium odoratum* Linn.		s
Mikania cordata (Burm. F.) B. L. Robinson		h
Struchium sparganophora (Linn.) O. Ktze		h
Connaraceae		
Agelaea obliqua (P. Beauv.) Baill.		s
Agelaea pseudobliqua Schellenb.		s
Agelaea sp.		l
Castanola paradoxa (Gilg.) Schellenb. ex Hutch. & Dalz.		s
Cnestis ferruginea DC		s
Connarus africanus Lam.		s
Manotes longiflora Bak.		s
Convolvulaceae		
Calycobolus africanus (G. Don.) Heine		l
Calycobolus heudelotii (Bak. ex Oliv.)		s
Ipomoea batatas (Linn.) Lam.		h
Ipomoea involucrata P. Beauv.		l
Ipomoea mauritiana Jacq.		h
Neuropeltis acuminata (P. Beauv.) Benth.		s
Neuropeltis prevosteiodes Mangenot		l
Neuropeltis sp.		l
Cyperaceae		

Cyperus sphacelatus Rottb.	h
Cyperus umbellatus Oliver	h
Mapania baldwinii Nelmes	h
Rhynchospora corymbosa (L.) Britt.	h
Scleria anomala (Steud.) S. Raynal	h
Scleria barteri Boeck.	h
Davalliaceae	
Nephrolepis biserrata (Sw.) Schott	h
Dichapetalaceae	
Dichapetalum angolense Chodat	s
Dichapetalum pallidum (Oliv.) Engl.	s
Dichapetalum toxicarium (G. Don) Baill.	s
Dilleniaceae	
Tetracera alnifolia Willd.	l
Tetracera potatoria Afzel. ex G. Don	l
Dioncophyllaceae	
Triphyophyllum peltatum (Hutch. & Dalz.) Airy Shaw	l
Dioscoreaceae	
Dioscorea alata Linn.	l
Dioscorea burkiliana J. Miège	l
Dioscorea cayenensis Lam.	l
Dioscorea multiflora Mart. ex Griseb.	l
Dioscorea smilacifolia De Wild.	l
Ebenaceae	
Diospyros canaliculata De Wild.	a
Diospyros chevalieri De Wild.	s
Diospyros mannii Hiern	a
Diospyros sanzaminika A. Chev.	a
Diospyros soubreana F. White	s
Diospyros vignei F. White	s
Euphorbiaceae	
Alchornea cordifolia (Schum. & Thonn.) Müll. Arg.	s
Bridelia grandis Pierre ex Hutch.	a
Claoxylon sp.	a
Cleistanthus polystachyus Hook. f. ex Planch.	s
Discoglypremna caloneura (Pax) Prain.	a
Drypetes aylmeri Hutch. & Dalz.	a
Drypetes gilgiana (Pax) Pax & K. Hoffm.	a
Drypetes klainei Pierre ex Pax.	a
Erythrococca anomala (Juss. ex Poir.) Prain	s
Macaranga barteri Müll. Arg.	s
Macaranga heterophylla (Müll. Arg.) Müll. Arg.	s
Macaranga hurifolia Beille	s
Macaranga sp.	a
Maesobotrya barteri (Baill.) Hutch.	a
Manniophyton fulvum Müll. Arg.	s
Mareya micrantha (Bent.) Müll. Arg.	s
Mildbraedia paniculata Pax	s
Oldfieldia africana Benth. & Hook. f.	a

Phyllanthus amarus Schum. & Thonn.	h
Phyllanthus discoideus (Baill.) Müll. Arg.	s
Phyllanthus muellerianus (O. Ktze) Exell	s
Pycnocoma macrophylla Benth.	s
Ricinodendron heudelotii (Baill.) Pierre ex Pax	a
Spondianthus preussii Engl.	a
Tetrorchidium didymostemon (Baill.) Pax. & Hoff.	s
Thecacoris stenopetala (Müll. Arg.) Müll. Arg.	s
Tragia benthami Bak.	l
Uapaca esculenta A. Chev. ex Aubrév. & Léandri	a
Uapaca guineensis Müll. Arg.	a
Uapaca paludosa Aubrév. & Léandri	a
Flacourtiaceae	
Caloncoba brevipes (Stapf) Gilg.	a
Homalium molle Stapf	a
Lindackeria dentata (Oliv.) Gilg.	s
Scottelia chevalieri Chipp.	a
Scottelia coriacea A. Chev. ex Hutch. & Dalz.	a
Soyauxia floribunda Hutch.	s
Gramineae	
Aeroceras zizanoides (Kunth) Dandy	h
Bambusa vulgaris Nees	h
Centotheca lappacea Desv.	h
Guaduella oblonga Hutch.	h
Leptaspis cochleata Thw.	h
Olyra latifolia Linn.	h
Oryza sativa Linn.	h
Panicum laxum Sw.	h
Panicum ovalifolium Poir.	h
Panicum parviflorum Lam. ex Spreng.	h
Paspalum conjugatum Berg.	h
Streptogyna crinita P. Beauv.	h
Guttiferae	
Allanblackia floribunda Oliv.	a
Garcinia afzelii Engl.	a
Garcinia kola Heckel	a
Garcinia ovalifolia Oliv.	s
Harungana madagascariensis Lam. ex Poir.	a
Mammea africana Sabine	a
Pentadesma butyracea Sabine	a
Humiriaceae	
Sacoglottis gabonensis (Baill.) Urb.	a
Icacinaceae	
Iodes liberica Stapf	l
Pyrenacantha vogeliana Baill.	l
Rhaphiostylis beninensis (Hook. f. ex Planch) Planch ex Benth.	s
Rhaphiostylis cordifolia Hutch. & Dalz.	s
Lauraceae	
Beilschmiedea bitehi Aubr.	a

Beilschmiedia mannii Benth. & Hook f.	a
Persea americana Mill.	a
Lecythidaceae	
Napoleonaea leonensis Hutch. & Dalz.	a
Napoleonaea vogelii Hook. & Planch.	s
Combretodendron macrocarpum (P. Beauv.) Keay	a
Leeaceae	
Leea guineesis G. Don	s
Liliaceae	
Chlorophytum alismaefolium Baker	h
Chlorophytum macrophyllum Aschers	h
Crinum giganteum Andr.	h
Haemanthus multiflorus Martyn	h
Linaceae	
Hugonia afzelii R. Br. ex Planch.	s
Loganiaceae	
Anthocleista vogelii Planch.	a
Strychnos aculeata Solered.	l
Strychnos dinklagei Gilg.	l
Strychnos usambariensis Gilg.	l
Malpighiaceae	
Acridocarpus longifolius (G. Don) Hook f.	s
Malvaceae	
Hibiscus esculentus Linn.	h
Urena lobata Linn.	s
Marantaceae	
Halopegia azurea K. Schum.	h
Marantochloa congensis (K. Schum.) J. Léonard & Mullend	h
Marantochloa filipes (Benth.) Hutch.	h
Marantochloa purpurea (Ridl.) Milne-Redhead	h
Megaphrynium distans Hepper	h
Sarcophrynium brachystachys (Benth.) K. Schum.	h
Thaumatococcus daniellii (Benn.) Benth.	h
Trachyphrynium braunianum (K. Schum.) Bak.	h
Melastomataceae	
Dissotis rotundifolia (Sm.) Triana	h
Memecylon fasciculare (Planch. ex Benth.) Naud.	s
Memecylon golaense Bak. f.	s
Memecylon guineense Keay	s
Memecylon lateriflorum (G. Don) Brem.	a
Memecylon memecyloides (Benth.) Exell	s
Tristemma coronatum Banth.	h
Tristemma sp. 1	h
Tristemma sp. 2	h
Meliaceae	

Carapa procera DC	a
Entandophragma angolense (Welw.)	a
Guarea cedrata (A. Chev.) Pellegr.	a
Lovoa trichilioides Harms	a
Trichilia heudelotii Planch. ex Oliv.	a
Menispermaceae	
Albertisia cordifolia (Mangenot & Miege) Forman	s
Dioscoreophyllum cumminsii (Stapf) Diels.	l
Kolobopetalum chevalieri (Hutch. & Dalz.) Troupin	l
Penianthus zenkeri (Engl.) Diels	a
Rhigiocarya racemifera Miers	l
Stephania dinklagei (Engl.) Diels	l
Tiliacora dinklagei Engl.	l
Triclisia macrophylla Oliv.	s
Triclisia sp.	l
Mimosaceae	
Acacia pennata (Linn.) Willd.	s
Albizia adianthifolia (Schum.) W. F. White	a
Albizia dinklagei (Harms) Keay	a
Albizia zygia (DC) J. F. Macbr.	a
Calpocalyx aubrevillei Pellegr.	a
Calpocalyx brevibracteatus Harms	a
Newtonia aubrevillei (Pellegr.) Keay	a
Newtonia duparquetiana (Baill.) Keay	a
Parkia bicolor A. Chev.	a
Pentaclethra macrophylla Benth.	a
Piptadeniastrum africanum (Hook. f.) Brenan	a
Moraceae	
Antiaris welwitschii Engl.	a
Chlorophora excelsa (Welw.) Benth.	a
Ficus capensis Thunb.	a
Sloetiopsis kamerunensis (Engl.)	s
Treculia africana Decne	a
Myristicaceae	
Pycnanthus angolensis (Welw.) Warb.	a
Pycnanthus sp.	l
Myrtaceae	
Eugenia calophylloides DC	s
Ochnaceae	
Lophira alata Banks ex Gaertn. f.	a
Ouratea affinis (Hook f.) Engl.	s
Ouratea duparquetiana (Baill.) Gilg.	s
Ouratea flava (Schum. & Thonn.) Hutch. & Dalz. ex Stapf	s
Olacaceae	
Coula edulis Baill.	a
Heisteria parvifolia Sm.	s
Octoknema borealis Hutch. & Dalz.	a
Ptychopetalum anceps Oliv.	s

Strombosia glaucescens Engl.	a
Orchidaceae	
Eulophia guineensis (Lindl.)	h
Nervilea petraea (Afzel. ex Pers.) Summerh.	h
Palmaceae	
Calamus deerratus Mann & Wendl.	l
Elaeis guineensis Jacq.	a
Eremospatha hookeri (Mann & Wendl.) Wendl.	l
Laccosperma opacum G. Mann & H. Wendl.	l
Laccosperma secundiflora Kuntze	l
Raphia hookeri Mann & Wendl.	l
Raphia sassandriensis A. Chev.	a
Pandaceae	
Microdesmis puberula Hook. f. ex Planch.	s
Panda oleosa Pierre	a
Papilionaceae	
Abrus precatorius Linn.	s
Baphia bancoensis Aubrév.	a
Baphia nitida Lodd.	a
Baphia polygalacea (Hook. f.) Bak.	s
Baphia pubescens Hook. f.	s
Dalbergia albiflora A. Chev. ex Hutch. & Dalz.	l
Dalbergia hostilis Benth.	s
Dalbergia saxatilis Hook. f.	s
Dalbergiella welwitschii (Bak.) Bak. f.	s
Desmodium adscendens (Sw.) DC	s
Desmodium velutinum (Willd.) DC	s
Erythrina vogelii Hook. f.	a
Leptoderris brachyptera (Benth.) Dunn	s
Leptoderris fasciculata (Benth.) Dunn	l
Millettia barteri (Benth.) Dunn	l
Millettia chrysophylla Dunn	l
Millettia rhodantha Baill.	a
Millettia zechiana Harms	s
Mucuna pruriens (Linn.) DC	l
Ostryocarpus riparius Hook. f.	s
Phaseolus lunatus Linn.	l
Phaseolus vulgaris L.	h
Platysepalum hirsutum (Dunn) Hepper	l
Passifloraceae	
Adenia cissampeloides (Planch. ex Benth.) Harms	l
Adenia lobata (Jacq.) Engl.	l
Crossostemma laurifolium Planch. ex Benth.	l
Pedaliaceae	
Ceratotheca sesamoides Endl.	h
Piperaceae	
Piper guineense Schum. & Thonn.	l
Piper umbellatum Linn.	s

Rapateaceae

Maschalocephalus dinklagei Gilg. & K. Schum.	h

Rhamnaceae

Lasiodiscus fasciculiflorus Engl.	s
Maesopsis eminanii Engl.	a
Ventilago africana Exell.	l
Ventilago sp.	l

Rhizophoraceae

Anopyxis klaineana (Pierre) Engl.	a
Cassipourea congoensis R. Br. ex DC	s
Cassipourea sp.	a

Rubiaceae

Aidia genipiflora (DC) Dandy	a
Bertiera bracteolata Hiern	s
Bertiera racemosa (G. Don) K. Schum.	s
Borreria intricans Hepper	h
Canthium arnoldianum (De Wild & Th. Dur.) Hepper	a
Canthium hispidum Benth.	s
Canthium rubens Hiern.	s
Canthium sp.	l
Cephaelis peduncularis Salisb.	s
Cephaelis yapoensis (Scnell) Schnell	s
Chassalia afzelii (Hiern) K. Schum.	s
Coffea humilis A. Chev.	s
Coffea liberica Bull ex Hiern	a
Corynanthe pachyceras K. Schum.	a
Craterispermum caudatum Hutch.	a
Cuviera acutiflora DC	s
Euclinia longiflora Salisb.	s
Gaertnera paniculata Benth.	s
Geophila afzelii Hiern.	h
Geophila hirsuta Benth.	h
Geophila neurodictyon (K. Schum.) Hepper	h
Geophila obvallata (Schumach.) F. Didr.	h
Heinsia crinita (A. F. Z.) G. Tayl.	s
Ixora laxiflora Sm.	s
Leptactina densiflora Hook. f.	s
Massularia acuminata (G. Don) Bullock ex Hoyle	s
Mitragyna ciliata Aubrév. & Pellegr.	a
Morinda longiflora G. Don	s
Mussaenda chippii Wernham	s
Nauclea diderrichii (De Wild. & Th. Dur.) Merrill	a
Oxyanthus formosus Hook. f. ex Planch.	s
Oxyanthus racemosus (Schum. & Thonn.) Keay	s
Pauridiantha afzelii (Hiern) Bremek.	s
Pavetta corymbosa (DC) F. N. Williams	s
Psychotria elongatosepala (Hiern) Petit	l
Psychotria guineensis Petit	a
Psychotria obscura Benth.	s
Psychotria psychotrioides (DC) Roberty	s
Psychotria sp.	l
Psychotria subobliqua Hiern	s
Psychotria vogeliana Benth.	s

Rothmannia longiflora Salisb.	s
Rothmannia whitfieldii (Lindl.) Dandy	s
Rutidea parviflora DC	s
Sabicea discolor Stapf	s
Sabicea ferruginea (G. Don.) Benth.	s
Sabicea sp. 1	l
Sabicea sp. 2	l
Sherbournia calycina (G. Don.) Hua	s
Tricalysia macrophylla K. Schum.	s
Tricalysia reflexa Hutch.	s
Tricalysia sp.	a
Trichostachys aurea Hiern.	s
Rutaceae	
Araliopsis tabouensis Aubrév. & Pellegr.	a
Citrus limon (L.)	a
Citrus reticulata Blanco	a
Citrus sinensis (L.)	a
Zanthoxylon macrophyllum Oliver	a
Sapindaceae	
Allophylus africanus P. Beauv.	s
Aporrhiza urophylla Gilg.	a
Blighia unijugata Bak.	a
Blighia welwitschii (Hiern) Radlk.	a
Chytranthus talbotii (Bak. f.) Keay & Thonn.	a
Deinbollia pinnata Schum.	s
Pancovia bijuga Willd.	a
Paullinia pinnata Linn.	l
Placodiscus pseudostipularis Radlk.	s
Sapotaceae	
Afrosersalisia afzelii (Engl.) A. Chev.	a
Aningeria robusta (A. Chev.) Aubrév. & Pellegr.	a
Chrysophyllum pruniforme Pierre ex Engl.	a
Chrysophyllum taiense Aubrév. & Pellegr.	a
Omphalocarpum ahia A. Chev.	a
Omphalocarpum elatum Miers	a
Tieghemella heckelii Pierre ex A. Chev.	a
Scrophulariaceae	
Lindernia diffusa (Linn.) Wettst.	h
Scytopetalaceae	
Scytopetalum tieghemii (A. Chev.) Hutch. & Dalz.	a
Selaginellaceae	
Selaginella versicolor Spring	h
Selaginella vogelii Spring	h
Smilacaceae	
Smilax kraussiana Meissn.	l
Solanaceae	
Solanum anomalum Thonning	s
Solanum macrocarpum Linn.	s

Solanum verbascifolium Linn.	s
Sterculiaceae	
Cola caricaefolia (G. Don) K. Schum.	s
Cola heterophylla (P. Beauv.)	s
Cola lateritia K. Schum.	a
Cola milleni K. Schum.	a
Cola nitida (Vent.) Schott & Endl.	a
Sterculia oblonga Mast	a
Sterculia rhinopetala K. Schum.	a
Sterculia tragacantha Lindl	a
Tarrietia utilis (Sprague) Sprague	a
Theobroma cacao Linn.	a
Thelypteridaceae	
Cyclosorus afer (Christ)	h
Thymelaeaceae	
Dicranolepis perseii Cummins	s
Tiliaceae	
Desplatsia chrysochlamys (Mildbr. & Burret) Mildbr. & Burret	a
Glyphaea brevis (Spreng) Monachino	a
Grewia barombiensis K. Schum.	s
Grewia bicolor Juss	s
Grewia pubescens P. Beauv.	s
Grewia sp.	s
Triumfetta rhomboidea Jacq.	s
Ulmaceae	
Trema guineensis (Schum. & Thonn.) Ficalho	s
Urticaceae	
Urera oblongifolia Benth.	l
Urera repens (Wedd.) Rendle	h
Verbenaceae	
Clerodendrum capitatum (Willd.) Schum. & Thonn.	s
Clerodendrum sp.	h
Clerodendrum umbellatum Poir	s
Clerodendrum volubile P. Beauv.	s
Vitex grandifolia Gürke	a
Vitex micracantha Gürke	a
Vitex oxycuspis Bak.	a
Vitex rivularis Gürke	a
Violaceae	
Rinorea ilicifolia (Welw. ex Oliv.) O. Ktze	s
Rinorea longicuspis Engl.	a
Rinorea oblongifolia (C. H. Wright) Marquand ex Chipp.	a
Vitaceae	
Ampelocissus gracilipes Stapf	l
Cissus aralioides (Welw. ex Bak.) Planch.	l
Cissus gracilis Guill. & Perr.	l

Cissus polyantha Gilg. & Brandt	l
Cissus producta Afzel.	l
Zingiberaceae	
Aframomum sceptrum (Oilv. & Hanb.) K. Schum.	h
Aframomum sp.	h
Costus afer Ker-Gawl	h
Costus deistelii K. Schum.	h

[1] Key to growth forms: a = tree; h = herb; l = liane; s = shrub.

Authorities were taken from Hutchison and Dalziel (1963) as far as possible. Other references used were Assi and Pfeffer (1975), Aubréville (1959, 1961), de Rouw et al (1990), Hoppe-Dominik (1989), Index Kewensis, Kramer and Green (1990), Letouzey (1963, 1986) and Mabberley (1987).

Appendix 7(a) Stomach contents

Stomach 1 - Collected 9/5/90 from Daobli. *C. maxwelli*.

Fruits:	*Pseudospondias microcarpa* (Meliaceae)	90g
Leaves:		4g
1 worm:		10g
Small fraction:		18g
Total weight:		122g

Stomach 2 - Collected 15/5/90 from Daobli. *C. maxwelli*.

Fruits:	*Combretum paniculata* (Combretaceae) x 1)	
	Tetrorchidium didymostemon (Euphorbiaceae))	1g
	Memecylon guineensis (Melastomataceae))	
	Scytopetalum tieghemii (Scytopetalaceae) x 32	9g
	Unidentified sp.	3g
Seeds:	*Pycnanthus angolensis* (Myristicaceae) x 1	2g
	Gilbertiodendron splendidum (Caesalpiniaceae))	<1g
Flowers:	"Gbourou-tou" (Oubi name)	2g
Leaves:		17g
Small fraction:		24g
Total weight:		58g

Stomach 3 - Collected 28/11/90 from Gouleako. *C. maxwelli*.

Fruits:	*Ficus vogeliana* (Moraceae) x 2	1g
	Unidentified, 4 - 6 spp.	4g
	Nauclea sp. (Rubiaceae)	7g
	Hugonia afzelii (Linaceae)	10g
	Jaundea pinnata (Connaraceae)	23g
Seeds:	*Xylia evansii* (Mimosaceae) (Djiaoh tou)	14g
Leaves:		1g
Small fraction:		14g
Total weight:		74g

Stomach 4 - Collected 28/11/90 from Gouleako. *C. maxwelli*.

Fruits:	*Dacryodes klaineana* (Burseraceae) x 3	2g
	Hugonia afzelii (Linaceae) x 3+	4g
	Chrysophyllum taiense (Sapotaceae) x 8+	7g
	Chrysophyllum pruniforme (Sapotaceae)	5g
	Unidentified (sp. 158) (Connaraceae) x 31+	11g
	Unidentified sp. x 1	2g
	Unidentified sp. x 12	10g
Small fraction:		33g
Total weight:		74g

Stomach 5 - Collected 18/12/90 from Gouleako. *C. dorsalis*.

Fruits:	*Dacryodes klaineana* (Burseraceae) x 13	10g
	Unidentified (sp. 158) (Connaraceae)	11g
	Unidentified fragments of large, fleshy fruit	5g
Seeds:	*Dacryodes klaineana* (Burseraceae) x 88	22g
	Unidentified fragments	5g
Leaves:		1g
Small fraction:		34g
Total weight:		88g

Stomach 6 - Collected 24/2/91 from Gouleako. *C. maxwelli* ♀.

Fruits:	*Dialium aubrevillei* (Caesalpiniaceae) x 2	1g
	Nauclea sp. (Rubiaceae)	1g
	Chrysophyllum pruniforme (Sapotaceae) x 3	7g
Seeds:	*Chrysophyllum taiense* (Sapotaceae) x 2	1g
	Bussea occidentalis (Caesalpiniaceae) x 3	5g
	Dacryodes klaineana (Burseraceae) x 2	1g
	Anthonotha fragrans (Caesalpiniaceae)	2g
	Parkia bicolor (Mimosaceae) x 2	1g
	Diospyros sp. (Ebenaceae)	7g
	Amphimas pterocarpoides (Caesalpiniaceae)	8g
	Cola lateritia (Sterculiaceae)	8g
Small fraction:		13g
Total weight:		55g

Stomach 7 - Collected 13/3/91 from Gouleako. *C. ogilbyi* ♀.
Largest item legume seed 47.5 x 31 x 7.5 mm.

Fruits:	*Dialium aubrevillei* (Caesalpiniaceae)	14g
	Cola lateritia (Sterculiaceae)	3g
	Parkia bicolor (Mimosaceae) x 1	3g
	Unidentified sp.	2g
Seeds:	*Amphimas pterocarpoides* (Caesalpiniaceae)	56g
	Diospyros sp. (Ebenaceae)	20g
	Diospyros sp. 2 (Ebenaceae) x 2	1g
	Unidentified legume x 3	7g
	Unidentified sp.	4g
Flowers:	2 unidentified spp.	1g
Leaves:		8g
Small fraction:		48g
Total weight:		167g

Stomach 8 - Collected 18/5/91 from Gouleako. *C. maxwelli*.

Fruits:	*Dialium aubrevillei* (Caesalpiniaceae)	29g
	Coelocaryon oxycarpum (Myristicaceae)	6g
	Nauclea sp. (Rubiaceae)	4g
	Scottelia chevalieri (Flacourtiaceae) x 4	2g

Seeds:	*Amphimas pterocarpoides* (Caesalpiniaceae)	11g
	Diospyros sp. (Ebenaceae)	26g
	Unidentified x 2	1g
Flowers:	*Diospyros* sp. (Ebenaceae)	1g
Leaves:		9g
Small fraction:		10g
Total weight:		99g

Stomach 9 - Collected 10/7/91 from Gouleako. C. maxwelli.

Largest item *Dialium aubrevillei* fruit (c. 25 x 25 mm).

Fruits:	*Dialium aubrevillei* (Caesalpiniaceae)	21g
Seeds:	*Dialium aubrevillei* (Caesalpiniaceae)	34g
	Diospyros sp. (Ebenaceae)	2g
Leaves:		1g
Small fraction:		42g
Total weight:		100g

Stomach 10 - Collected 8/91 from Gouleako. *C. dorsalis*.

Largest item *Chrysophyllum taiense* fruit, 30.8 x 17mm.

Fruits:	*Chrysophyllum taiense* (Sapotaceae)	23g
	Dialium aubrevillei (Caesalpiniaceae)	10g
	Thaumatococcus daniellii (Marantaceae)	2g
	Nauclea sp. (Rubiaceae)	7g
	Unidentified sp. ("fah-mlon, pod like okra)	1g
	Unidentified sp.	1g
Seeds:	*Chrysophyllum taiense* (Sapotaceae)	1g
	Dialium aubrevillei (Caesalpiniaceae)	22g
Leaves:	*Alchornea cordifolia* (Euphorbiaceae))	12g
	Others)	
Small fraction:		37g
Total weight:		79g

Stomach 11 - Collected 31/8/91 from Gouleako. *C. maxwelli*.

Fruits:	NONE.	
Flowers:	*Anthocleista nobilis* x 1)	1g
	Unidentified sp.)	
	Unidentified sp.)	
Leaves:		3g
Small fraction:		25g
Total weight:		29g

Appendix 7(b) Leaf species reported to be eaten by duikers

Species	**Family**	**Growth form**[1]
Monodora tenuifolia	Annonaceae	a
Landolphia membranacea	Apocynaceae	l
Landolphia owariensis	Apocynaceae	l
Anchomanes difformis	Araceae	h
Culcasia parviflora	Araceae	h
Culcasia saxatilis	Araceae	h
Mondia whitei	Asclepiadaceae	l
Dacryodes klaineana	Burseraceae	a
Griffonia simplicifolia	Caesalpiniaceae	s
Myrianthus libericus	Cecropiaceae	a
Salacia zenkeri	Celastraceae	l
Parinari aubrevillei	Chrysobalanaceae	a
Agelaea pseudobliqua	Connaraceae	s
Castanola paradoxa	Connaraceae	s
Dichapetalum toxicarium	Dichapetalaceae	s
Cleistanthus polystachyus	Euphorbiaceae	s
Mareya micrantha	Euphorbiaceae	s
Napoleonaea leonensis	Lecythidaceae	a
Pycnocoma macrophylla	Euphorbiaceae	s
Spondianthus preussii	Euphorbiaceae	a
Leea guineensis	Leeaceae	s
Strychnos dinklagei	Loganiaceae	l
Halopegia azurea	Marantaceae	h
Megaphrynium distans	Marantaceae	h
Thaumatococcus daniellii	Marantaceae	h
Guarea cedrata	Meliaceae	a
Tiliacora dinklagei	Menispermaceae	l
Ouratea duparquetiana	Ochnaceae	s
Heisteria parvifolia	Olacaeae	s
Ptychopetalum anceps	Olacaceae	s
Microdesmis puberula	Pandaceae	a
Baphia nitida	Papilionaceae	a
Ostryocarpus riparius	Papilionaceae	s
Cuviera acutiflora	Rubiaceae	s
Pavetta corymbosa	Rubiaceae	s
Afrosersalisia afzelii	Sapotaceae	a
Cola heterophylla	Sterculiaceae	s
Cola lateritia	Sterculiaceae	a
Sterculia oblonga	Sterculiaceae	a
Rinorea longicuspis	Violaceae	a

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[1] a = tree, h = herb, l = liane, s = shrub

Appendix 8 Density estimates from line transect censuses

a) Theory[1]

Line transects differ from plot methods of census in that the analysis allows for some objects to go undetected, which is inevitable when dealing with secretive animals or small camouflaged objects. Four basic assumptions for the method, in order of decreasing importance, are as follows:-

1. Transect lines are distributed randomly with respect to objects being censused.
2. Points directly on the transect line are always detected.
3. Distances are measured accurately.
4. Sightings are independent events.

The density of objects is given by

$$D = n / 2L\hat{a}$$

where D = density
n = number of objects detected
L = transect length
$\hat{a}$ = effective strip width.

The effective strip width is the only unknown variable, and is determined by assuming that the probability of detection of an object is proportional to the perpendicular distance (x) from the transect:-

$\Pr(\text{detection}) \propto x$ or $g(x)=\Pr(\text{detection} \mid x)$

From the first assumption above, that all objects on the transect are detected, it follows that

When $x=0$, $g(0)=1$.

The effective strip width $\hat{a} = \int g(x)\,dx$.

This is the area under the detection curve, representing all widths and the probability of detection at each, up to a maximum distance w (which can be set either as the largest value of x recorded, or at a lower value after analysis in order to truncate the data and discard outliers).

However, it is easier to calculate $1/\hat{a}$ than $\hat{a}$ itself, so we must look at another probability density function (pdf). If $f(x)$ denotes the pdf of the perpendicular distance data, then $f(x) = g(x) / a$, which is $g(x)$ scaled to integrate to 1.

$\rightarrow$ $f(0) = 1/a$, so $\underline{D = nf(0)/2L}$.

This is the equation used in the main analysis for density; the key issue is how to find $f(0)$.

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[1] Based on Burnham et al (1980)

b) DISTANCE - a computer program

DISTANCE (Laake et al, 1993) is a program to calculate densities from line or point transect censuses using any of four key functions (Uniform, half-normal, exponential and hazard-rate), with a variety of adjustment terms in order to find the best fit to the data. All of the functions are 'model robust' (flexible) and 'pooling robust' (can be pooled over unknown factors affecting density, eg. different habitat types).

For a given key function, the program finds the optimum number of adjustment terms using a likelihood ratio test (LRT); it then compares key functions by estimating Akaike's Information criterion (AIC) and selecting the model with the lowest value. It also provides a p-value for a χ^2 goodness-of-fit test by comparing observed and expected frequencies in each distance grouping (Buckland et al, 1993). If data are entered in separate sample groupings for separate days of the census, the samples are compared to determine the sample variance.

Options within the program include grouping data into distance intervals in order to smooth the curve and correct for inaccurate measurements, and truncating data to simplify modelling by discounting outliers or a long 'tail'. Options were selected by looking at a histogram of frequencies of perpendicular distances for each data set to identify any irregularities, and if necessary running successive analyses until a close fit could be found.

c) Analysis of daytime censuses of duikers (IET only)

L = 32779 m, n = 41, 15 samples. Distances grouped 0-4, 5-9, 10-14, 15-20, 21-27, 28-40, 41-50; 5% right truncation.

Histogram (Figure 8.1(a)) shows movement away from centreline, so second analysis carried out with left truncation of 4 m (following Buckland et al, 1993; recommended improvement but still likely to underestimate true density).

Uniform + cosine model selected (AIC = 138).
D = 34 (95% C.I. 23 - 50).
With left truncation, **D = 36 (95% C.I. 24 - 56).**

d) Analysis of night-time censuses of duikers (IET only)

L = 23283 m, n = 46, 10 samples. Distances grouped 0-4, 5-9, 10-14, 15-19, 21-24. See Figure 8.1(b).

Half-normal model selected (AIC = 141.13).
D = 101 (95% C.I. 68 - 150).

Analysis of data for C. maxwelli only:
Half-normal + hermite polynomial model selected (AIC = 85.92). n = 31. **D = 102 (95% C.I. 58 - 179).**

e) Analysis of pellet-group density (IET and Gouleako, 1990 and 1991)

IET, 1990 - L = 3930 m, n = 43, 4 samples. Distances grouped 0-7, 8-14, 15-21, 22-28, 29-35, 36-45, 46-55, 56-65, 66-75, 76-85, 86-95, 96-105, 106-125, 126-175, 176-195; 30% right truncation. See Figure 8.2(a).

Hazard rate + cosine model selected (AIC = 131.14).
D = 19,267/km^2 (95% C.I. 4,320 - 85,940).

IET, 1991 - Analyses attempted with distances grouped and ungrouped, right truncations 0% to 30%. Programme could not find a good fit to data ($p(\chi^2)<0.000$). Figure 8.2(b) shows a large number of observations on the transect itself, but no steady decrease in frequency of observations with distance from the transect; thus a basic assumption of the analysis technique is violated.

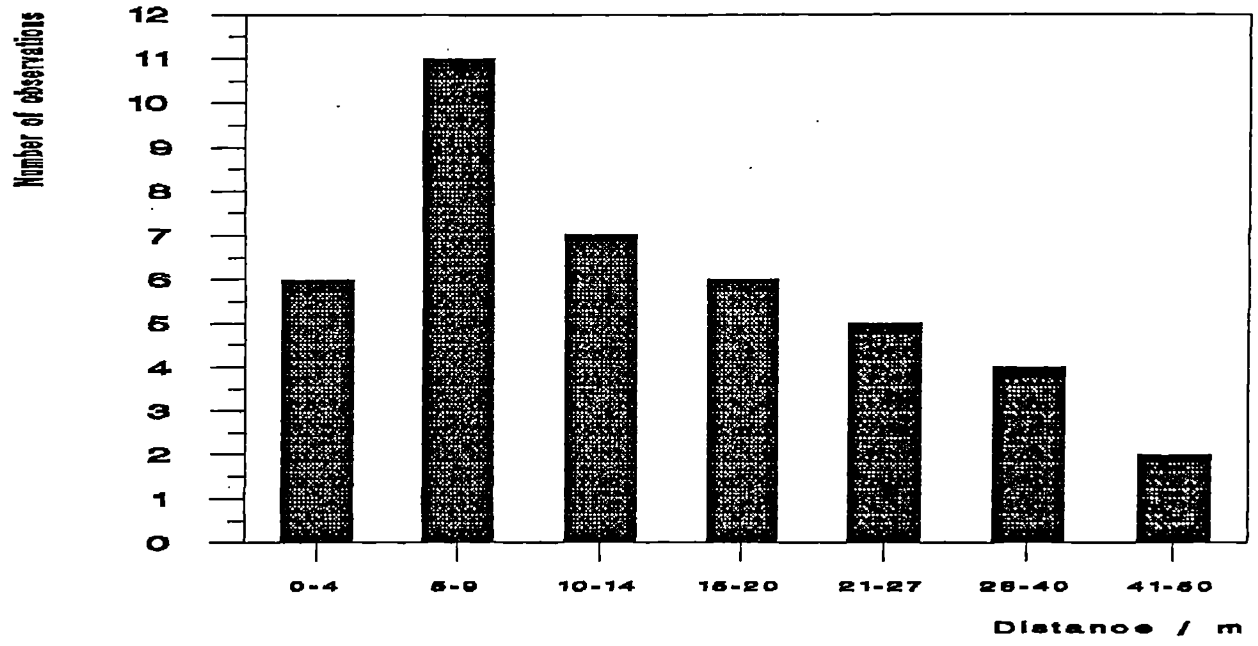
Gouleako, 1990 - L = 4411 m, n=161, 8 samples. Distances grouped 0-2, 3-5, 6-8, 9-11, 12-14, 15-17, 18-22, 23-27, 28-37, 38-47, 48-57, 58-67, 68-87, 88-107, 108-147, 148-197, 198-247; 10% right truncation. See Figure 8.2(c).

Hazard rate + cosine model selected (AIC = 747.8).
D = 74,612 (95% C.I. 40,837 - 136,320).

Gouleako, 1991 - L = 8117 m, n = 37, 12 samples. Histogram 8.2(d) shows no decrease in frequency of observations with distance from transect; thus a basic assumption of the analysis technique is violated.

Figure 8.1 Transects of duikers - Number of observations at different distances from the transect

a) Daytime, IET



b) Night-time, IET

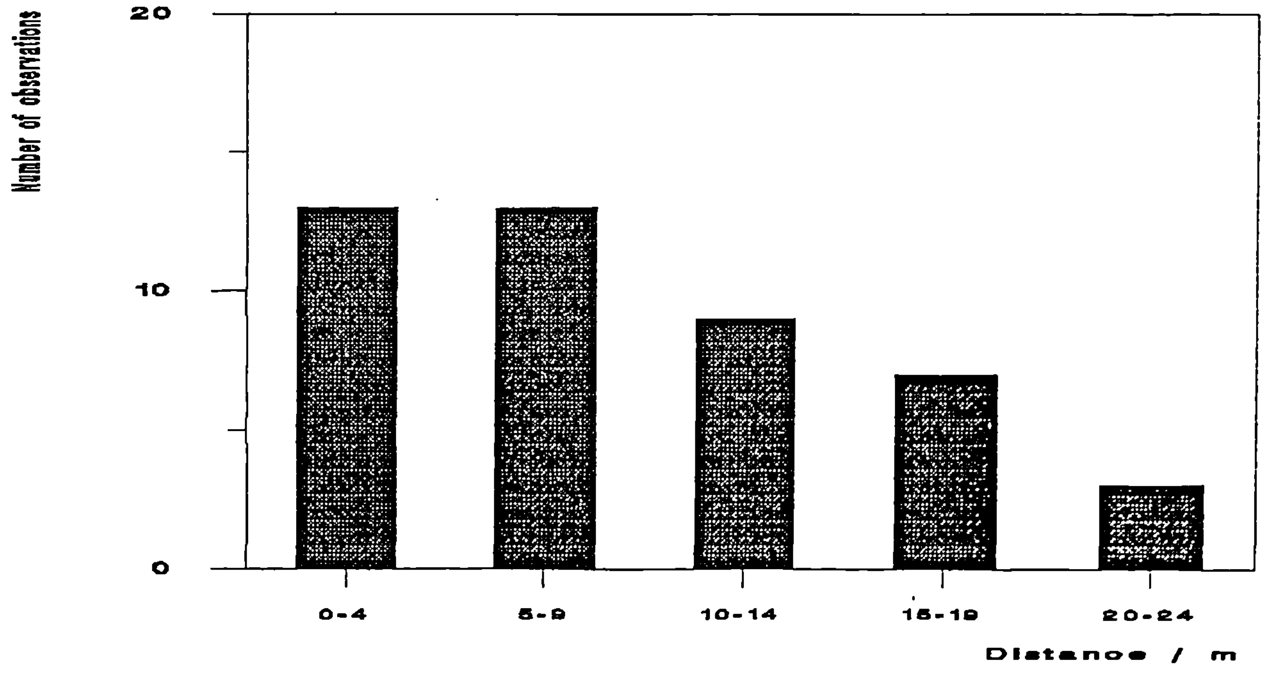
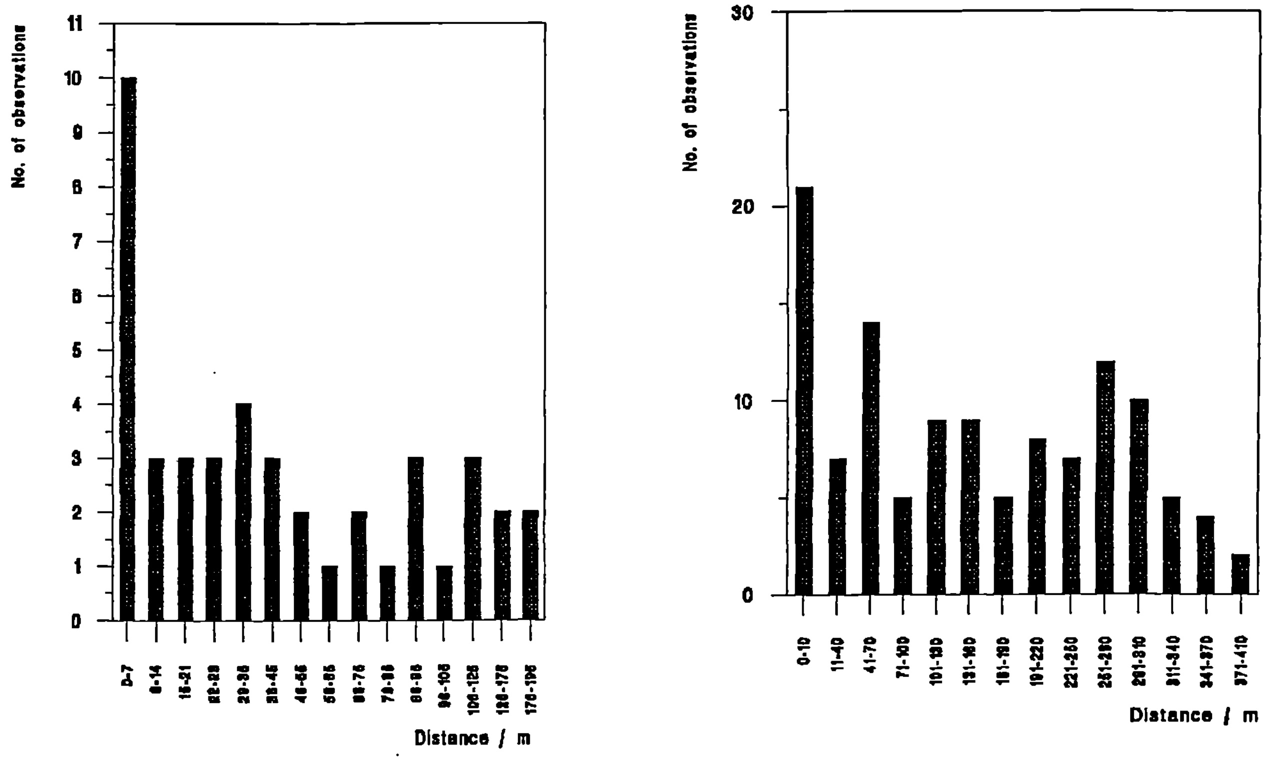


Figure 8.2 Pellet transects - Number of observations at different distances from the transect


a) IET, 1990

b) IET, 1991

c) Gouleako, 1990

d) Gouleako, 1991