ON THE ECOLOGY AND BEHAVIOUR OF THE AFRICAN ELEPHANT: THE ELEPHANTS OF LAKE MANYARA

By

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CHAPTER 1 — INTRODUCTION

INTRODUCTION

The history of elephant problems

The ability of the African elephant Loxodonta africana africana, (Blumembach, 1789) to transform the landscape from woodland and forest to grassland is now well known. Laws (1970b) remarked “after man himself, probably no other animal has had as great an effect on African habitats as the African bush elephant”. Another drastic agent is fire, which by preventing tree regeneration, makes irreversible changes in many areas where burning cannot be controlled. Consequently, “elephant problems” are now a feature of most National Parks and Reserves in which elephants live. Case histories of elephant-habitat interactions have been documented in the Kruger National Park in South Africa (Van Wyk & Fairall, 1969); the Zambezi (Uys, 1972) and Luangwa Valleys (Dodds & Patton, 1968; Hanks, 1971) of Zambia, and the extensive literature covering Kenya, Uganda and Tanzania is reviewed by Laws (1970b).

In most places the habitat modification is thought to have resulted from local increases of elephants within the National Parks and Reserves concurrent with drastic reduction in their total range. Their former range throughout Africa and its continued decrease is well recorded. Neolithic rock etchings show that elephants ranged through the Sahara about 5,000 – 11,000 years before the present (Mauny, 1957). In classical times they were found along the Mediterranean seaboard from the Straits of Gibralter to Carthage (Pliny) and may even have ranged into Syria in about 1,000 A.D. (Sherborn, 1957*)*. As recently as the sixteenth century they were found as far south as the Cape of Good Hope (Van Riebeck, 1653, in Shortridge, 1934). Most of the reduction in range can probably be attributed, to man’s expansion and methods of hunting. The Boer farmers and ivory hunters exterminated elephants in most areas south of the Limpopo (Gordon-Cumming, 1850; Bryden, 1903; Shortridge, 1934), until by the turn of the century only minute pockets were left in the Kaokoveldt, Knysna, and Addo Forests, and in the Kruger National Park (Stevenson-Hamilton, 1929). Having destroyed the elephant populations of South Africa, hunters turned their attention to East and Central Africa (Selous, 1908; Neumann, 1898; Bell, 1923). Fears were expressed that the African elephant was doomed to rapid extinction, (Lydekker, 1894; Simon, 1962) and this opinion was widely held for many years (Maxwell 1925).

Other factors than man may also have played a decisive role. It is probable that climatic changes may have forced the elephant out of the Sahara area, although

Laws (1970b) has suggested the possibility that the elephants themselves may have been largely responsible for the conversion of woodlands to desert, and that the Lake Rudolf area and Tsavo National Park in Kenya may provide recent and current examples of this process.

In East Africa the elephant decrease followed the South African pattern, until the introduction of Game Laws at the turn of the century, when indiscriminate shooting of elephants for the ivory trade gradually came under control (Simon, 1962). Their range however continued to decrease. In Uganda it has been estimated that elephants in 1929 ranged over 70 per cent of the country but by 1959 this area had decreased to 17 per cent (Brooks & Buss, 1962).

The actual buildup in numbers within the Parks and Reserves has been harder to measure, partly due to the late stage at which aerial counts were first introduced and partly because differences in technique of aerial censuses often made it difficult to compare census results of different years with confidence (E. Afr. Agri. For. J., 1969, Special issue 39). However, it is almost certain that present elephant densities have greatly increased locally because of drastic reduction in their range, and census data of varying degrees of certainty support this (Glover, 1963; Buechner, et al., 1963; Buss & Savidge, 1966; Pienaar, et. al. 1966; Lamprey et. al. 1967; Watson & Bell, 1969; Savidge, 1968; Laws & Parker, 1968; Laws, 1969b; Field, 1971).

The management dilemma

The problems posed by elephant-induced woodland destruction have caused a deep schism in the ranks of scientists and National Park administrators regarding the role which man should play in regulating elephant numbers. The views I have heard expressed, mainly amongst National Parks staff, against the culling of elephants as a solution may broadly be summarised as follows: the National Parks were created as sanctuaries to save the remnants of Africa’s wildlife. The killing of elephants is repugnant, and would set a precedent for new forms of utilization incompatible with the present rationale and policy. A primary objective of National Parks policy is to maintain the ecosystem in as ‘natural’ a state as possible, despite the admitted difficulties of defining this term. In view of man’s mistakes in the past, a conservative policy should be adopted. It is hoped that ‘natural’ regulation will eventually control the elephant population and restore a balance. That this natural regulation might take the form of a population crash is not disputed. This view does not admit that habitat changes are irreversible, but argues that large oscillations in sizes, distributions, and compositions of elephant and woodland populations are probably a ‘natural’ feature of their dynamics. To intervene and regulate elephant populations might freeze an ecosystem at one stage in its development, causing the perpetuation of a particular habitat type, and interruption of a long-term cycle. In particular it is feared that the large short-term profits to be gained from a reduction cropping scheme might release political pressure for the National Parks to be run as meat factories rather than sanctuaries.

The opposing arguments which support the culling of elephants run as follows: the creation of the National Parks was in itself an 'unnatural' event as the boundaries did not enclose complete ecosystems, or even complete population ranges of the resident animals. The possible disappearance of woodland communities is incompatible with the National Park objective of preserving habitats in all their diversity (Parker pers. comm.). In former days a balanced woodland elephant cycle probably depended on unlimited space, where elephants could then move out of a devastated woodland area into a new one, leaving the first to recover, but the present National Parks are units too small to allow this effect (Laws, 1970b). A barricade of human settlement prevents any large scale dispersal. Even so, it is possible that natural regulation might be adequate if the elephants had merely been confined, but the situation is actually worse as the elephant populations have been compressed. It is argued that the adjustments observed in fertility and early calf mortality (Laws & Parker, 1968), would be too slow to prevent the irreversible habitat effects of the high standing crop of elephants, composed mainly of long lived adult animals. At worst these changes could lead, within an area, to complete extinction of woodlands, forests and their associated fauna, a lowering of species diversity, carrying capacity, and energy turnover, and even to the extinction of elephants themselves in the very areas set aside expressly for their survival (Laws & Parker, 1968). It is suggested that enough is now known about the dynamics of elephant populations, their habitat requirements, and elephant induced habitat change to justify culling in order to conserve the environment (Laws, 1970b), and that the standing crop of elephants should be reduced by a large fraction, to a level at which natural regulation might control the population in accordance with the carrying capacity of the land (Laws, 1972). If natural regulation should then prove to be inadequate to contain intrinsic increase, as opposed to increase through immigration, then sustained yield cropping, subsequent to the initial capital reductions, could be introduced.

The controversy has not yet been resolved with any unanimity of opinion. A choice between action and inactivity has to be faced, as the consequences of either might be irreversible.

The need for research

At the basis of the dispute is the difficulty in defining objectives, a matter of human values and not of scientific objectivity. In addition there is little known about what natural factors may have regulated elephant populations in the past or whether they may do so in the future. Predictions of future population levels, whether of woodlands or elephants, can at the best only be tentative. Clearly the following are key questions:

1. Will the high density elephant populations naturally decrease without culling and without irreversible habitat changes?

2. Can the National Parks accept the risk of huge, possibly irreversible, changes in woodland vegetation and its dependent animal populations including elephants?

3. What would be the ecological, political and aesthetic ramifications of a cropping policy?

This thesis will confine itself to an investigation of the natural regulation of elephant population attempting to isolate the most important factors influencing fertility and mortality. Publications to date suggest that fertility and early calf mortality might be the most important controlling factor in areas such as North Bunyoro in Uganda, (Lass & Parker, 1968; Laws, 1969a). The recent die-off of elephants in Tsavo (Sheldrick, 1972), suggests that irregular massive mortality, affecting all age classes, might potentially control populations in other areas (Glover, 1972).

Three proximate factors which might be important in affecting fertility and mortality and which might be density dependent have been suggested: nutritional stress, heat stress and social stress (Laws & Parker, 1968; Laws, 1970a). Figure 1.1 summarizes the established processes (in boxes) and hypothetical causal pathways (unboxed) leading from a human population increase to a declining elephant population.

Each of the proximate factors might be density dependent. Nutritional stress might depend on the availability of browse, and McCullagh (1969) has demonstrated nutritional deficiency in the elephant population of the deforested Murchison Falls National Park. Heat stress would depend on the availability of shade and in Tsavo, where canopy cover has been greatly reduced in recent years (Laws, 1969b), circumstantial evidence supports the possibility of heat stress killing starving animals (Mr. S. Trevor, pers. comm.). Both types of stress would be density dependent, as the browse and canopy cover reduction would be proportional to elephant density.

Laws and Parker did not define what forms of social stress they envisaged which might act as density dependent controlling factors, but it has been shown in many species that, under conditions of increased density, care of the young may deteriorate, social aggression may increase, and reproductive behaviour may be inhibited (Wynne–Edwards, 1962).

Social stress might also depend on the habitat, in that competition might increase under conditions of resource scarcity. Social stress might however be more directly density dependent if aggression were related to frequency of inter–individual or inter–group encounters, which would he expected to rise with density. This would be particularly true if elephants were normally territorial animals, and would provide a social pressure for spacing and dispersal. If dispersal were frustrated, increased social stress might result, with consequences of decreased fertility and increased mortality. Calhoun (1962) has demonstrated in a laboratory system how overcrowding mice can cause such an increase in their territorial and aggressive interactions which eventually results in the complete inhibition of reproductive behaviour in both sexes.

Although the elephant social organisation has been worked out in some detail from cross–sectional inferences (Buss & Smith, 1966; Laws & Parker, 1968), and a number of levels of social organisation have been suggested, such as Family Unit, Extended Family Unit, Clan and Population, no long-term study had been made to observe the stability of these groupings, their social interactions, or their formation and splitting. I therefore set myself the following objectives:

Objectives

1. To make a comparative study of elephant ecology and behaviour in a particular area as a contribution to the general knowledge of elephant problems.

2. To study the dynamics of elephants' social organisation as a necessary background to the problems of elephant population regulation.

Choice of Study Area

I chose the Lake Manyara National Park as a study area in 1965 for the following reasons:

1. The National Parks Management was aware of the need for research on which to base their policy.

2. The Park offered particularly interesting conditions within the context of East Africa as a whole. The habitats appeared more variable than any comparable area with an elephant problem hitherto studied, and superficially it appeared to be an ideal ecosystem for elephants with rich alkaline pasture, swamps, forest, woodland, escarpment, dense bushy areas and a rich diversity of plant species (Greenway & Vesey–Fitzgerald, 1969). The elephant density of more than 5/Km^2 (14/sq. ml.) (Watson & Turner, 1965) was the highest value published at that time for any wildlife area in Africa. This high density in the midst of apparently optimal habitat suggested that to some extent the possible effect of social density on reproduction could be isolated from the effects of habitat conditions and food availability.

   Fire, normally integral to any elephant problem, had been absent for five years previous to 1965. Therefore this variable could be ignored when examining the dynamics of woodland mortality and regeneration in relation to elephant feeding behaviour.

3. A population estimate for the Park, of 420 elephants within 30 square miles (Watson & Turner, 1965) appeared small enough to allow the study to be based on the method of individual recognition.

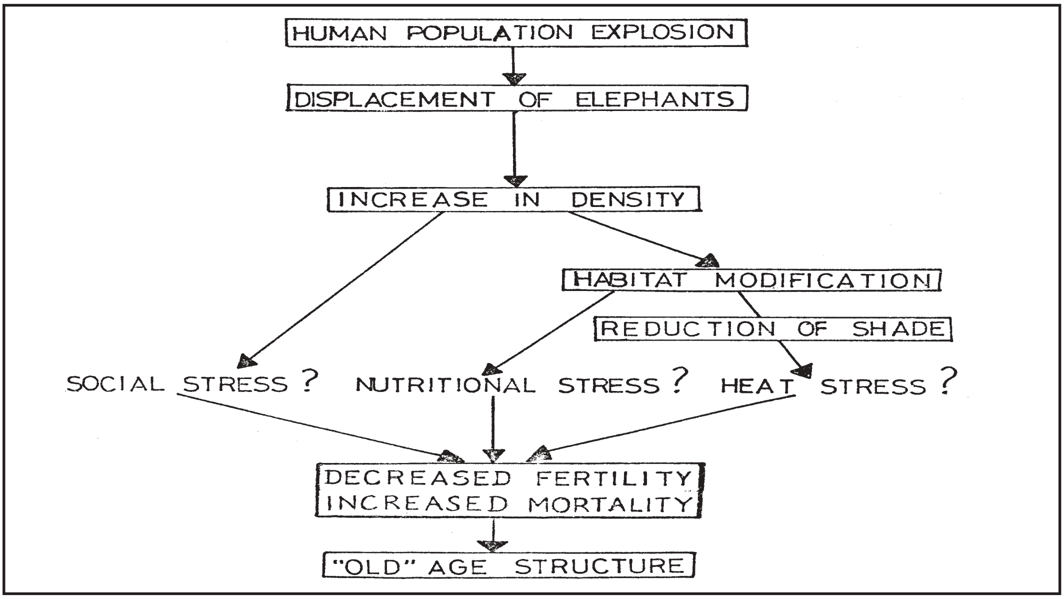
4. The beginnings of a dispute between an "activist" and "laissez–faire" school already existed. Watson & Turner

(1965) knew that elephants stripped and gouged bark off the trees but not to what extent. On the grounds of exceptional density and biomass alone, they suggested that the elephant and buffalo populations exceeded the carrying capacity of the Park. Vesey–Fitzgerald expressed a contrary view at the time (later published 1969), pointing out that even in the height of the dry season many pastures were unutilized by buffalo, and the tree damage caused by elephants was not serious. No information existed either on year round elephant densities, nor on rates of habitat change.

Research Programme

The research programme was designed to investigate each stage of the classical elephant problem as illustrated in Figure 1.1, under the Manyara conditions. This thesis follows the same order. Chapter Two describes the study area and habitats of Manyara together with the local history of human increase and displacement of elephants. Chapter Three describes methods of general application, and Chapter Four elephant numbers and densities around the year. In Chapter Five, the social organization, in spatial terms is examined, and Chapter Six discusses social interactions, particularly in relation to reproductive success. In Chapter Seven, elephant–habitat interactions are described and Chapter Eight considers the population dynamics, with a discussion of the effects of density, social behaviour and habitat conditions. In Chapter Nine, the Manyara elephant problem is summarized, tentative predictions and recommendations on various courses of action are made.

Figure 1.1 Hypothetical causation of declining elephant population.



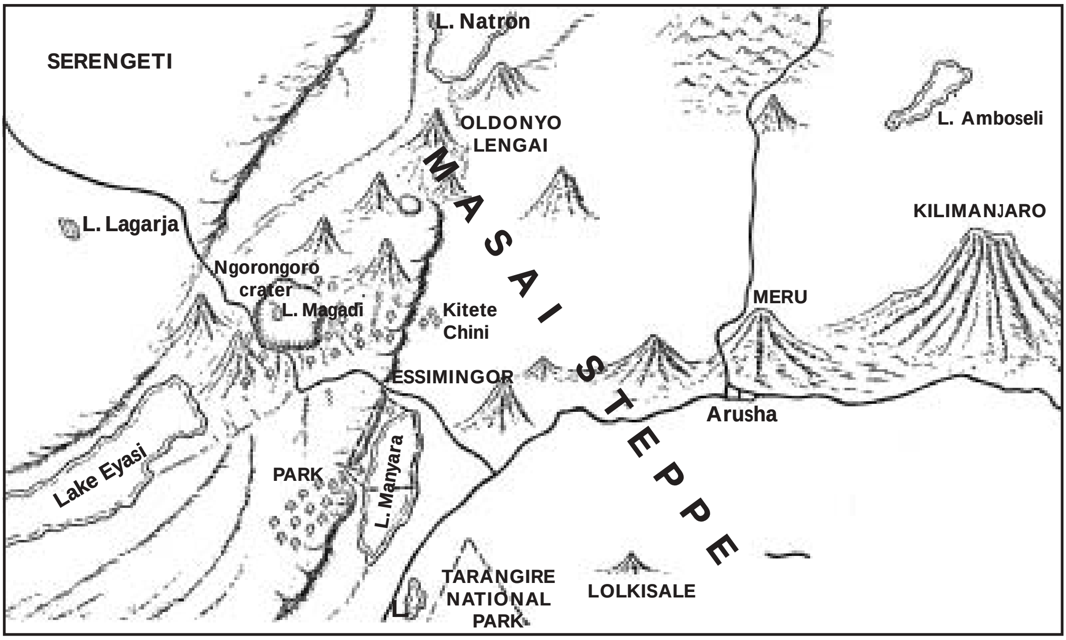
CHAPTER 2 — STUDY AREA AND HISTORY

STUDY AREA AND HISTORY

Location

Lake Manyara, the smallest of the three great Rift Valley Lakes of Northern Tanzania, some 430 km^2 in area, lies at the foot of the Western escarpment of the Great Rift Valley which runs in a North–South direction (see Fig. 2.1 opposite). The escarpment at the North end of the Lake forms a line of cliff faces 800 m high, dissected by deep precipitous gorges. Further south erosion has smoothed the rugged outline into steep rounded slopes. At long. 35^0 51'E, lat. 03^0 21'S, the lake is 960 m. (3150 ft.) above sea level, and forms the sump of an inland drainage system of some 10,360 Km^2 (4000 square miles). The water is alkaline with the dissolved salts of river water left behind by evaporation. About 50 km. to the north–west above the escarpment are the forests of the Ngorongoro Crater Highlands, a range of extinct volcanoes and a vital water catchment area for the surrounding farms and the National Park. 65 km. to the north along the Rift Valley is the still active volcano Oldonyo Lengai, with the immense Lake Natron beyond. To the east is the Masai steppe and the volcanic mountains of Essimingor and Monduli; beyond is Mt. Meru, 195 km. away, with the regional capital of Arusha at its foot. In the South, swamps give way to plains and more mountains, and in the

Figure 2.1 Location of Lake Manyara National Park.



South–West above the escarpment is the Marang forest, another vital catchment area supplying the River Endabash in the South of the Park.

Area

Lake Manyara National Park is situated on the West of the Lake and includes some of the cliffs and slopes and a narrow strip of land below thorn which runs along the Lake shore, Fig. 2.1. Altogether the Park is approximately 310 km^2 in area including about two-thirds of the Lake, but the Lake level varies, and in 1970 only 85 Km^2 (33 square miles) was dry land. The width of this strip at its narrowest was 1.5 Km. and at its broadest 5 km., and it had a length of 31.25 km.

Geology

The Geological Survey of Tanzania have mapped this area, and a brief account by Pickering (1968) summarizes the geological history and formation. From his account it appears that the crater highlands were formed by volcanic activity some 5 to 1 million years before present (B.P.). After the collapse of the Ngorongoro centre of eruption, with the formation of a large caldera, volcanic activity declined, although new volcanoes Oldonyo Lengai and Kerimasi developed further north. Gradually erosion attacked the sides of the Crater Highlands and the newly formed scarps. The streams draining these slopes began to cut deep valleys, which remain as spectacular gorges. Lake Manyara received gravels, sands, and mud derived from the highlands, and extensive beds of limestone were laid down in the Lake. The new volcanoes distributed a great deal of lime–rich ash which consolidated to give calcareous tuff. Consequently the eastern sides of the Crater Highlands are mainly basaltic lavas with a local cover of brown earth, and pumiceous tuff. The soils below the escarpment within the Park are derived from the volcanic material transported from above, *and* are classed by Greernway & Vesey-Fitzgerald (1969) as ‘hard pan’ or ‘plain’ soils. Pickering comments that “volcanic rocks generally give very fertile soils”.

In the Highlands the superficial layer of soil is full of pore spaces, and the underlying lava has many cracks and holes so that water has no difficulty in entering these rocks. Much of the rain, which falls seasonally, soaks through the soil and percolates into the lava. Water passes very slowly, and lower down the slopes moisture oozes out of the red soil, together with water issuing from springs throughout the dry season. Some of these springs lie in the agricultural area to the West of the Park above the escarpment. Pickering (1968) comments that “the agricultural wealth of this district largely depends upon these springs and seepages just as much as it does on the fertile, red volcanic soil”. Perennial waters also issue from the lavas at the foot of the Gregory Rift Scarp, and this natural irrigation allows the development of forest and swamp formations within the Park which would not otherwise be possible under the existing climatic regime (Greenway & Vesey–Fitzgerald, 1969).

The dependence of the Park on the Ngorongoro water catchment area cannot be over-emphasised. Already dangerous forms of land use, over-grazing and cultivation on steep slopes, have resulted in gully erosion in parts of the catchment area which are deforested. The run off of water is no longer delayed by thick vegetation, and between 1966 and 1970 the quantity of soil deposited in the river deltas within the Park increased to levels beyond all previous local recollection. “If the Ngorongoro forests were destroyed”, Pickering remarked, “then the soil would lose its spongy nature; the rain would no longer be able to soak into the soil and the rocks beneath it; hence the springs would dry up and the farmlands would become valueless”. It might also be added that many of the most important forest and woodland habitats within the Manyara National Park on which the present high biomass of game animals depend, would probably become arid, with profound consequences for the vegetation arid animal populations.

Climate

The climate of this area is equable for the tropics; temperatures vary between a mean annual high of 26.5^0 – 29.5^0C to a mean annual low of 15.5^0 - 18.5^0C. (Tanganyika Atlas 1967). The prevailing wind is from the South-East and brings with it rain-bearing clouds which tend to precipitate when they are forced up by the escarpment. A bank of cloud builds up at about 2,300 m. (7,000 ft.) which usually persists all morning except in the months of January and February, when the skies tend to be clear all day. The cloud layer greatly reduces direct radiation and hence the temperature.

Annual rainfall is subject to fluctuations varying between 380 and 1,270 mm. per year (1961–1970, Mto-wa-Mbu). In common with the rest of East Africa long term weather cycles have probably exerted a strong effect on the distribution and types of habitat. From October to December the ‘short rains’ fall lasting until January. Not much rain falls in January or February, the ‘short dry season’, but from March until May, the bulk of annual precipitation comes during the ‘long rails’. From June until September, ‘the long dry season’, there is very little or no rain at all.

Four and a half years of monthly records from four storage gauges appear in histograms in Fig. 2.2. It is clear that the long dry season in the middle of the year demarcates one period of rainfall from the next. The short dry season is less marked than in other areas. Annual totals were therefore calculated from the mid-point of one year to the mid–point of the next. The mean annual rainfall from mid-1966 to mid-1970 averaged 763 mm. for gauge (1), 788 mm. for gauge (2), and from mid-1967 to mid-1970, 891 mm. for gauge (3), and 1219 mm. for gauge (4) showing a gradient increasing from North to South, corresponding to a similar increase in escarpment height from 1219 m. to 1829 m. a.s.l. (4000–6000 ft.).

Figure 2.2
Monthly rainfall

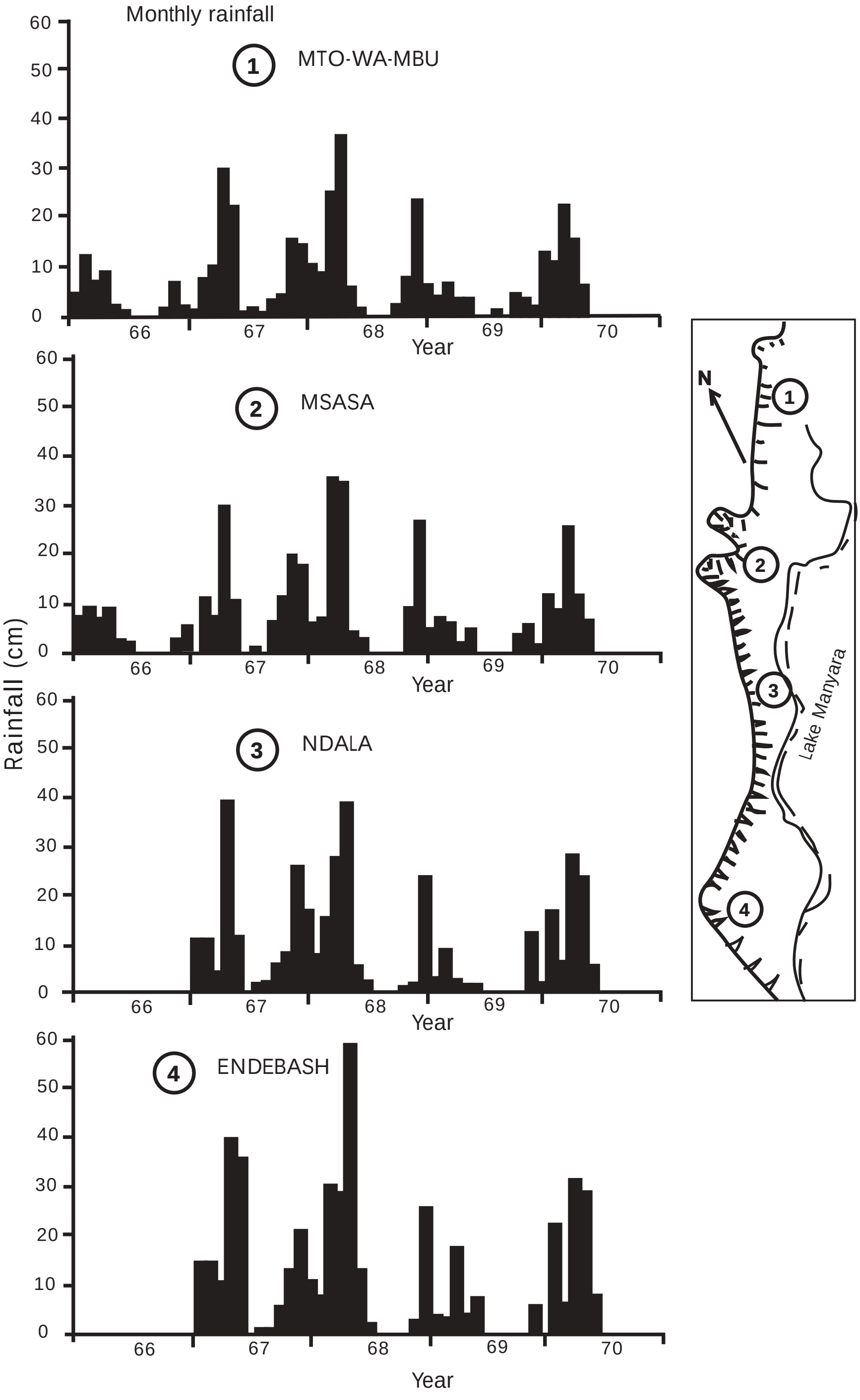
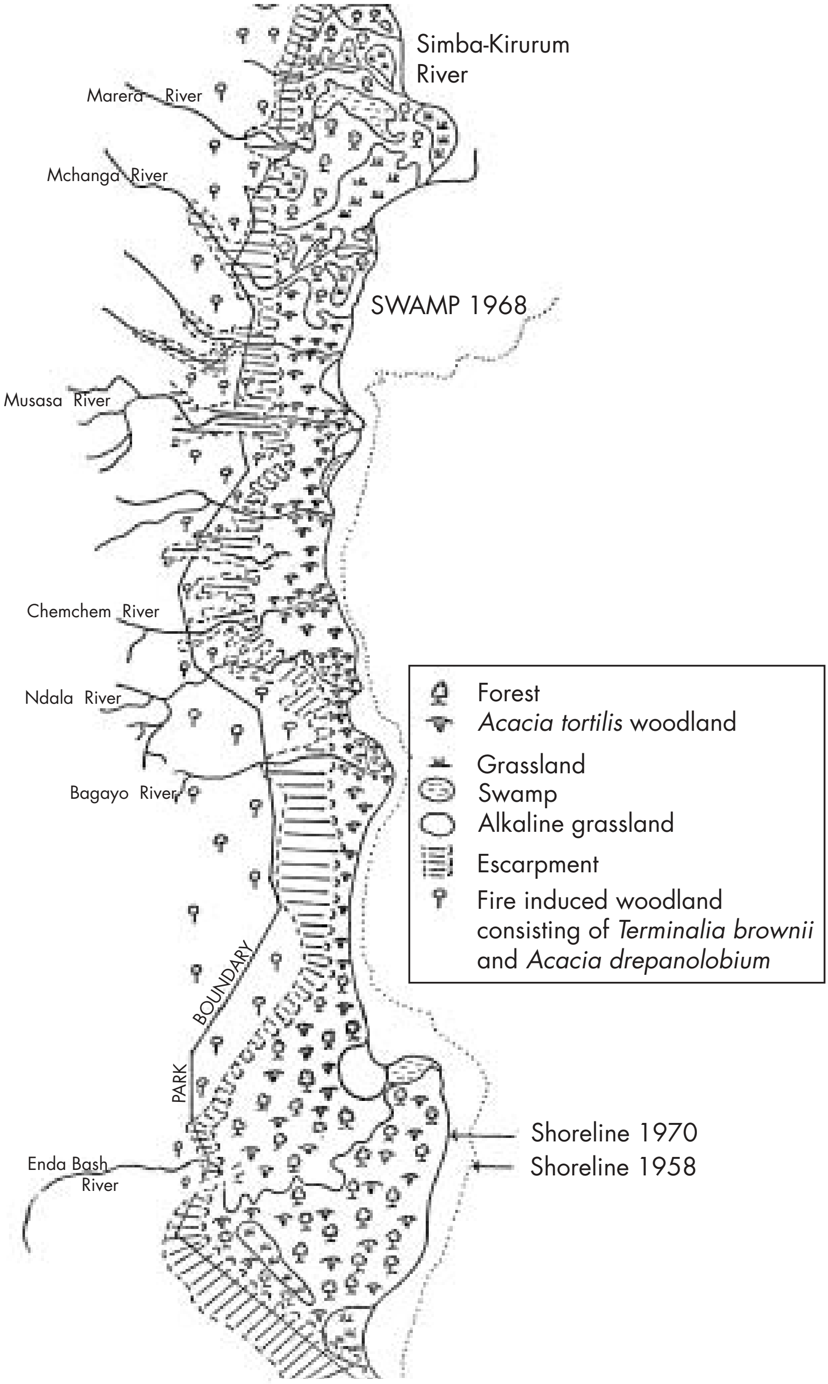


Figure 2.3
Vegetation map of Lake Manyara National Park.



Lake Level

The lake level shows fluctuations corresponding to the rainfall, but the changing course of the Tarangire River, which in some years flows into Lake Burungi to the South-East, and in others into Lake Manyara, may also be an important factor. During former pluvial eras the Lake has been much higher than its present levels (Dr. Livingstone, pers. comm.). In 1892 when Baumann first discovered the lake, it was relatively low, with only two lagoons of water left at either end of a shining basin of crystalline salt. At times the lake dried up altogether, as happened in 1929, 1934, 1941, 1954, and 1960 (Watermeyer & Elliott, 1943; Greenway & Vesey-Fitzgerald, 1969). It does not take long for the lake to refill however, and record high levels were recorded in 1942, and again in 1964 (ibid), both following dry periods. After the exceptionally heavy rains of 1967–68 the lake rose to the highest level within living memory, reaching a record high point in 1970. Acacia tortitis trees, which I estimated to be more than 70 years old (Chapter 7) with a circumference of 240 cms. were inundated and drowned. The effect on the vegetation is discussed below.

Vegetation

The Park is characterized by an unusually large variety of habitats for so small an area. This diversity is related both to the East–West change in altitude from Lake shore to escarpment heights, and to the North–South gradation in rainfall and ground water. The most important habitats are found below the escarpment and these sustain the bulk of the Park's biomass throughout the year.

A full description of habitat types, and their species composition, is given by Greenway & Vesey-Fitzgerald (1969), which requires only a few additional notes. Fig. 2.3 is a vegetation map on a scale of 1:100,000 and shows the distribution of habitat types in 1970. The details of the relative frequency and dynamics of the woodland species will be given in Chapter 7. I have followed the nomenclature of Greenway & Vesey-Fitzgerald (1969).

The vegetation of the National Park is greatly affected by ground water seepages, a fluctuating lake level, elephants, and in the past by fire. In the North is the ground water forest, owing its existence to springs emerging from below the cliffs. I have sub-classified this forest into two types: the first is 'Trichilea forest' which is found along the drainage lines containing many different species, of which the tall, dark green Triochilea roka dominates, forming a thick closed canopy in places. On higher more arid ground between the drainage lines, "Acacia forest" is found, in which the species A. albida and A. xanthophloea predominate. The two types of forest show up clearly on aerial photographs with 'Trichilia' dark grey and 'Acacia' light grey, and therefore can be accurately mapped.

Where the drainage is impeded, swamps develop in the middle of the forest, with a mixed composition of Cyperaceae sedges and Typhaceae, reed mace. At the outlet of the Simba and Kirurum Rivers into the North West corner of the Lake, a pure stand, 10 Km^2 in area, of the reed Typha angustifolia used to grow, until in 1968 the lake rose and inundated the entire swamp. For a period of nine months huge floating islands of matted Typha were blown around the Lake. Some of these fetched up on the Park shores further South where they began to establish new colonies. A few green shoots sprouted among the rotting mass, but their success was short–lived as elephants waded out into these islands and ate both shoots and decomposing stems until none were left. In this way a favoured habitat of elephants, and hippopotamus, comprising 9 per cent of the Park's vegetations surface area, disappeared entirely, and had not re-appeared by 1970, when the Lake level was slightly lower.

The flooding also affected a flat belt of alkaline pasture, mud flats, and salt deposits with an area of 14.5 km^2 in 1958. At that time it supported about 700 wildebeeste (Morgan–Davies 1961), and provided pasture for elephants, and buffalo which grazed the short grasses, Odyssia jaegeri and Sporobolus spicatus, and the sedge, Juncel1us laevigatus. By 1968 this habitat had almost entirely disappeared under the water. Altogether the Park's vegetation surface area was reduced by about 23 per cent within 10 years.

Below the escarpment Acacia tortilis woodland: pre-dominates in the middle of the Park. Apart from a few Balanites aegytiaca and Acacia sieberiana, with fringes of riverine trees along the watercourses, the woodlands consist of pure stands of Acacia tortilis. The thickness of these stands varies and according to Greenway and Vesey-Fitzgerald (1969) is related to subterranean water. In alkaline areas of poor drainage, patches of grassland have developed dominated by the tall Sporobulus consimilis. On higher shelves of sandy soil beneath the escarpment the woodlands give way to an open zone of thickets. The Acacia tortilis woodlands are in a state of rapid decline due to damage caused by elephants. This will be fully described in Chapter 7.

In the Southern bulge of the Park, watered by the Enderbash River, is a flat area of mixed woodlands, remnants of forest types and a large swamp. The river meanders and often changes its course. The sandy banks are covered in a thick sward of Cynodon dactylon which remains green for most of the long dry season. The commonest trees are Acacia sieberiana, Balanites aegyptiaca, Ziziphus pubescens and Croton macrostachys. In many places the aromatic shrub Ocimum suavi grows in dense thickets between the trees, to a height of 2.5 m. (8 ft.). This habitat severely limits visibility on the ground, although elephants can still be seen quite readily from the air. As this shrub impedes the movement of a human being, but offers little resistance to elephants, rhino, and buffalo, footpaths in this area can be hazardous.

Further South the Park narrows again and hot springs issue from below the cliffs at Maji Moto. The escarpment on the South–West boundary rises to 935 m. above the

Lake. Its slopes are well forested and, although very steep, the elephants have made paths winding between cliff faces right up to the summit. In this way they have direct access to 212 Km^2 (82 square miles) of the Marang Forest, an area about two and a half times that of the Park, with a completely different species composition of high altitude forest trees. During the 1968 rains massive landslides down the escarpment slopes cut wide strips through the vegetation and across the elephant paths.

Further North along its length the escarpment is cut by deep river gorges, and the more permanent rivers have a fringe of gallery forest. In -the middle of the Park, the escarpment is surmounted by hilly broken parkland. Further inland the first human settlements begin just outside the boundary, and soil erosion can be seen on all sides.

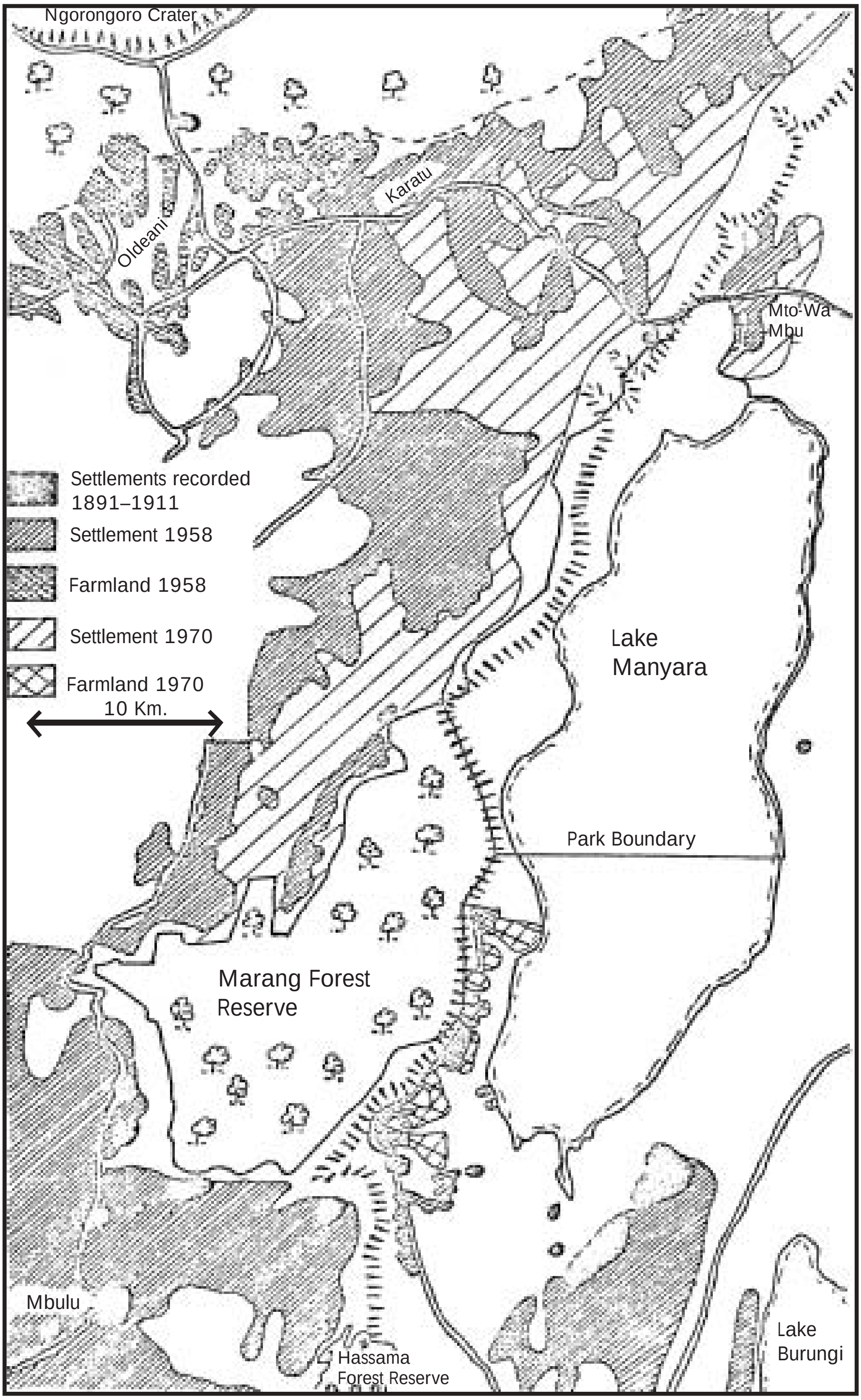
The escarpment slope has woodland thicket, where it is steep and fire protected, with trees with colourful papery bark such as Commiphora and Sterculia species, and many baobabs Adansonia digitata. In some areas fires still occasionally creep down the slopes from the settlements above, against the prevailing wind. In these places grass covers the whole slope. North of the Musasa River as far as the present Hotel, the escarpment is cliff-like, and is surmounted by a flat grassy plain which burns every year. This is poor pasture with only a few fire resistant trees such as Acacia drepanolobium and A. seyal. The soil is also highly leached (Dr. J. Weir pers. comm.) and the cattle of the Wambulu need a regular salt supplement to their diet which is brought up by their herders from the Lake shore below.

Human Population Increase

Around the Park are areas of dense human settlement. Archaeological finds 1 Km. North of the present Park in the valley of Miwaleni, show that man is no recent invader in these areas (H. Sassoon pers. comm.). Nevertheless human populations densities have risen sharply only in the last seventy years. This increase is partly due to modern medicine and partly to the cessation of tribal conflict following colonial rule. The Ngorongoro area and Mbulu highlands above the present Park have been a scene of tribal strife since the Masai wrested control of the Ngorongoro Crater from the Iraqw (Wambulu) tribe in the seventeenth century (Dr. A. Jacobs per. comm.). The area above the Park formed a tribal no-man's-land, grazed by the cattle of both Iraqw and Masai but settled by neither.

I have been able to trace the increase in settlement from historical records. Between 1892 and 1914 the area was criss-crossed and thoroughly mapped by numerous German explorers. Place names given in the earliest record of Farler (1882), who interviewed Swahili traders returning to the coast, can be located on the German maps of Baumann (1894); Obst (1915) and Uhlig (1909). A British military map of 1916 condensed all former records on a 1:300,000 scale. Areas of human settlement have been transferred to a modern map and appear

Figure 2.4
Human population map of Lake Manyara area.



in black in Fig. 2.4. These few settlements had expanded to cover most of the area by 1958 when the first aerial survey was made. The peaceful Iraqw cultivators, protected by colonial government, were able to settle the highland areas without disturbance. European settlers also arrived in the Oldeani area in 1926 and cultivated coffee and wheat on the fringe of the Montane forest. (Fosbrooke, 1972). Unlike the Masai who seldom hunt, the Iraqw and European farmers were responsible for wholesale eradication of the natural fauna in their areas, as well as causing gully erosion. Between 1957 and 1967 Mbulu district, which includes this area, showed a 49 per cent increase in human population (Tanzania Atlas 1967). Elephants which Farler's (1882) traders had reported as very plentiful vanished, presumably into the highland forest or into the thick vegetation below the Rift Wall.

To the south-west of the Lake are the Wambugwe people, living on the salt flats. Both they and the Masai on the plains of the Rift Valley were unable to penetrate the area immediately below the escarpment due to the prevalence of human and bovine trypanosomiasis. In 1955 the colonial government granted about 80 Km^2 of the swamp and woodland on the south-west Lake shore to European farmers, on the condition that they would cut down the trees in order to create a tsetse fly barrier, thus preventing the spread of trypanosomiasis (a disease carried by the tsetse fly). According to Mr. Craig Thom who farmed there from 1955 to 1970 the elephant population had previously extended continuously below the escarpment. Over the following ten years these "farmland" elephants, numbering about 400, were shot out or harassed until they moved into the Marang Forests and the "Park" area.

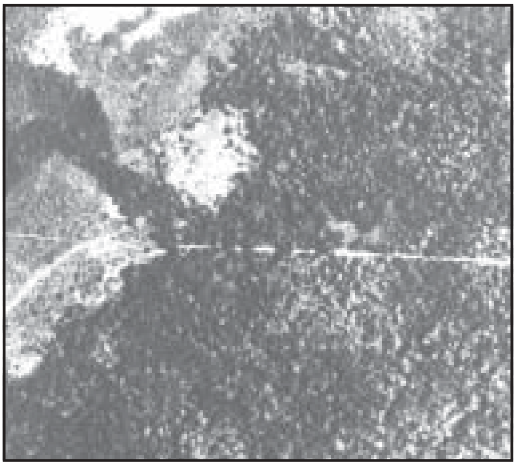
The present day village of Mto-wa-Mbu north of the Lake is also of recent origin and did not exist at the turn of the century (Baumann 1894). In 1920 the first African to farm below the Rift Wall set up a small–holding or shamba (Arens, 1972). This strip of fertile land, formerly unavailable because of the Masai, swiftly filled up with immigrants from all over East Africa, particularly after the building of a new main road in 1930, and by 1967 numbered 3,414 people (Arens, 1972). Interviews with locals revealed that previously this area was heavily forested and the elephants ranged throughout the village, penetrating 15 miles north of the present boundary to the Kitete Chini Forest, and from there up into the Ngorongoro Crater Highlands.

The Park area remained free of human settlement in these years, but the Ground water Forest was exploited for timber and almost all <u>Chlorophora excelsa</u> (African mahogany) were removed. In 1957 a game reserve was declared and in 1960 the National Park was officially gazetted (Morgan-Davies, 1961). The village expanded right up to the boundaries and the remaining unprotected forest was cut down (Fig. 2.5). Elephants and villagers came into conflict. A deliberate effort was made to drive elephants out of' the village area into the Park and to "teach" them the boundary which ran along the main road by shooting any individual that set foot on it. The Park Warden remarked on the speed with which the survivors learned to avoid the area (Morgan-Davies, 1961). In 1967 an electric fence was installed, which by 1970 had effectively sealed the village boundary of the Park.

In 1970 the aerial photography was repeated as part of this study and showed a tremendous increase in human settlement on all sides of the Park, particularly above the escarpment. Elephants at this time had been alienated from their range to the north, west and south of the Park and movement in and out of the Park had almost ceased except across the Marang Forest boundary (Fig. 2.6). The sharp rise in the Lake level throughout the 1960's had further concentrated the elephants. I estimate that the total range of the Manyara elephants has decreased by over 75 per cent in less than 50 years.

The human increase and elephant range decrease in the Manyara area are typical of elephant problems all over East Africa. Although the overall elephant numbers have almost certainly declined along with the range, the local density within the protected areas has probably increased, but no reliable documentation exists before the aerial count of Watson & Turner (1965). The remaining wild area available to the elephants including the Marang Forest is 297 Km^2 of which only 85 Km^2 is within the National Park. Large scale seasonal movements from the Marang Forest into the Lake Eyasi basin are still reported to occur every rainy season by the Forest guards, but it is unlikely that these will continue as settlement increases.

Figure 2.5: Aerial photo coverage, Mto-wa-mbu.



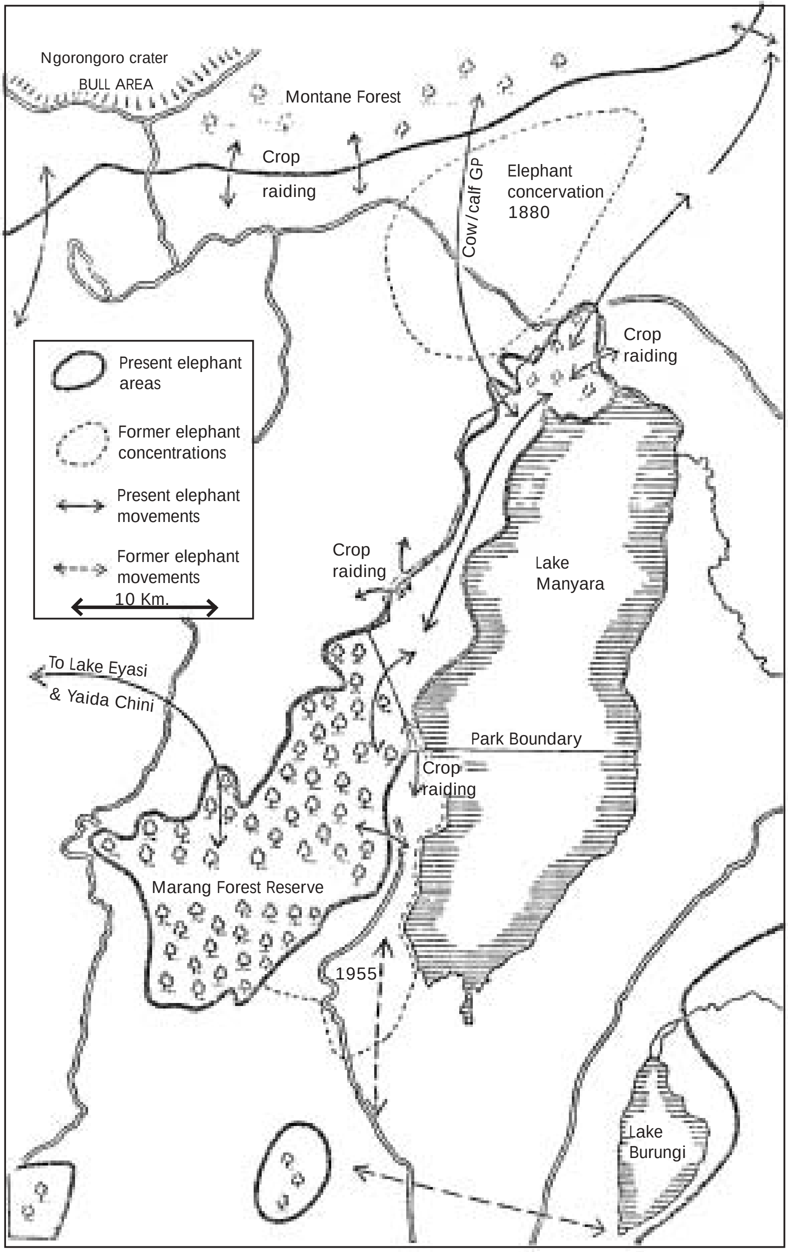
A. Mto-wa-Mbu forest, 1958.

B. Mto-wa-Mbu forest, 1970. The park bounderies runs along the road.

In the early 1960's an event of profound ecological importance began to exert a long term effect on the Manyara area. A tourist hotel was built on the escarpment overlooking the Park. The hotel is entirely dependent on the attraction of the wildlife and its profits have demonstrated that the existing ecological regime is the most economic form of land use for the area at present within the National Park boundaries.

Perhaps even more important is a gradually more positive attitude of the Mto–wa–Mbu villagers, who obviously enjoy the free game viewing trips, provided by the Park Warden, and who derive substantial economic benefits from employment as the Park's staff. The existing ecology of the L.M.N.P. depends entirely on the tolerance of man and cannot be realistically considered in isolation of this factor.

Figure 2.6 Elephant population map.



CHAPTER 3 — METHODS

METHODS

The methods described in this chapter of individual recognition, coverage of ground, radio–tracking and age estimation were of general application to different aspects of the study such as numbers and density, social organisation, and interaction and population dynamics. As this Chapter deals exclusively with methodology and does not contribute to the central argument it may be skipped and referred to later. Methods for the study of specific problems will be discussed in the relevant Chapters.

Individual Recognition

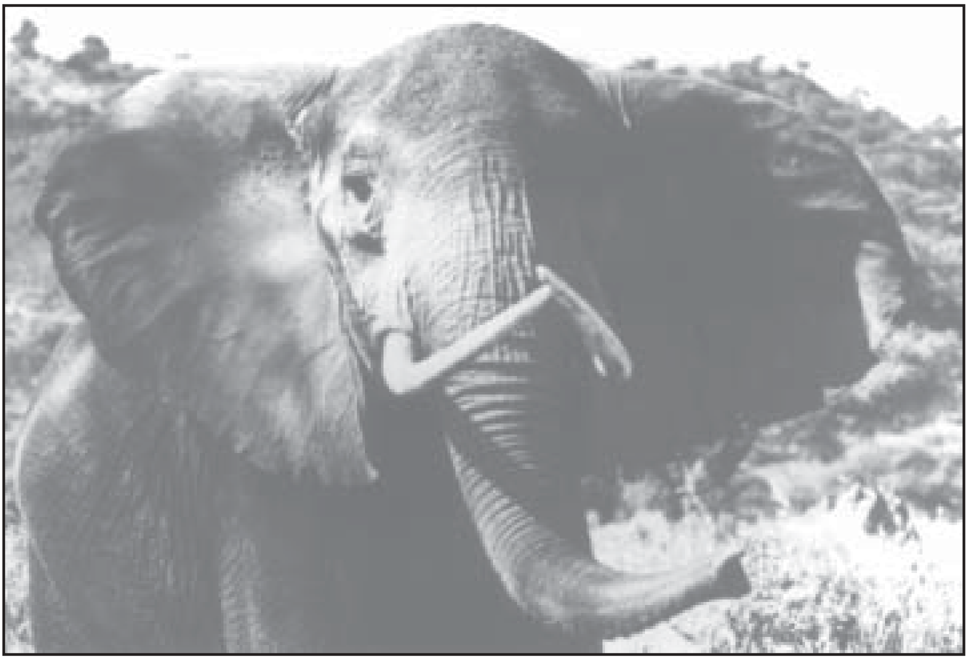
Various techniques have been described for marking elephants, for example by painting or branding them after immobilization (Pienaar, 1966, 1970), or by bombing them with paint bombs (Croze, 1969). However, paint and brand marks may become quickly covered in mud and soon disappear (Hanks, 1969). A number of wild mammalian populations have been studied using methods of individual recognition that do not rely on marking and which avoid disturbance; for example prairie dogs (King, 1955), coatis (Kaufmann, 1962), chimpanzees (Goodall, 1962), zebras (Klingel, 1965), lions (Makacha & Schaller, 1969) giraffe (Foster, 1966), and rhinoceros (Goddard, 1966). Striking individual elephants have also been repeatedly recognised previous to this study; such as 'Ahmed' of Marsabit mountain (Mr. B. Woodley, pers. comm.), 'Odinga' of the Amboseli Game Reserve in Kenya (Mr. D. Western, pers. comm.), the 'Tangi monster' (Laws & Parker, 1968), the 'Lord Mayor of Paraa' (Bere, 1966), of the Murchison Falls National Park, and several elephants in the Kibale Forest Reserve (Wing & Buss, 1970). These were all large distinctive animals but small cows and even calves are also individually recognizable.

Throughout its life, the ears of an elephant are in motion, acting as cooling organs (Appendix 2). From time to time they are torn when they get caught on thorn bushes. Some elephants seem to have weaker, more friable ears than others, which become very serrated with a continually changing outline, but generally the ear pattern alters very slowly (see Fig. 3.1). The outline of each has distinctive cuts, notches, and tears; also the pattern of blood vessels, veins and arteries, which can be seen underlying the skin is unique for each ear. Most elephant ears have holes in places, some have warts, and the general shape may vary.

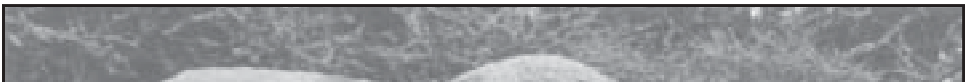
The tusks also exhibit great variety. Generally, in a young animal the tusks are straight but pointing outwards. As the animal grows older the tusks usually curve inwards. The depth of curve, thickness and alignment provide differences which the human eye can readily perceive. One tusk is often higher than another, and with

Figure 3.1

Sarah, March 1966.

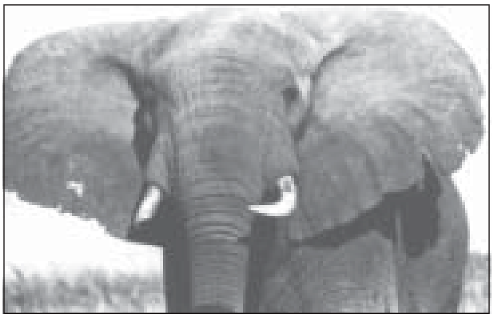


Sarah, March 1970.

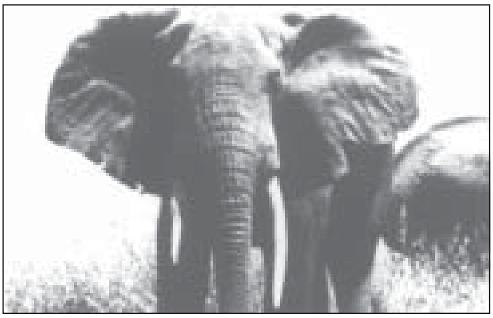


Distinctive notches, veins and small holes in the ear changed very little over four years. The tusks, however grew a few centimetres.

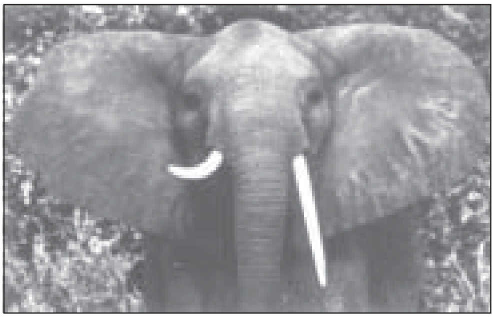
Figure 3.2 Recognition photographs.



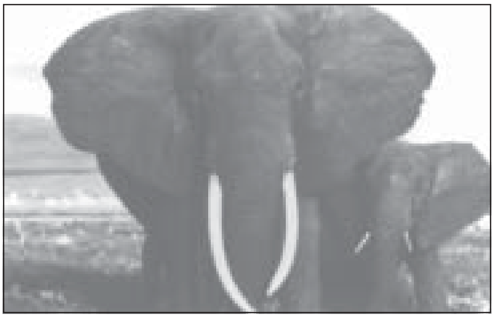
M 53 Mhoja's bull



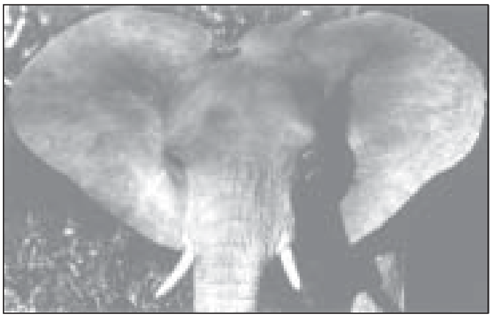
M 7 Cyclops



JEY F.U. Jane Eyre



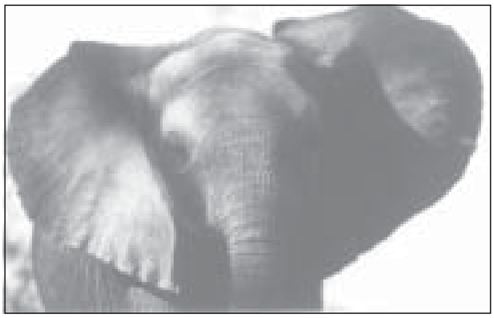
LEO F.U. Leonora



BOA F.U. Fiametta

VIC F.U. Mkali

SAR F.U. Sarah's C.l



BOA F.U. Diana's C.1 (b. JUL .66)

practice it is possible to detect asymmetry even in very closely matched tusks. The rate of wear shapes the tusks unevenly. One is usually blunter than the other as it is used more commonly, as a master tusk. Some elephants have very rounded points to their tusks, probably because the ivory is soft and wears down fast. A tusk may also chip or break, and frequently distinctive grooves are seen near the tip where the elephant habitually pulls grass over the same place.

These tusk and ear characteristics provided the necessary variation for a system of identification. Large animals tended to be obviously distinct, but calves were often similar, distinguishable only by minute differences. The most efficient method of recording these details was photographically, so that even a brief glimpse of an elephant could be recorded instantly and accurately. Full length frontal photographs of an elephant with its ears maximally extended could be obtained simply by approaching an elephant in full view until it adopted this posture as a mild threat.

Photographing elephants one at a time I gradually built up a register which by mid–1967 included over 400 elephants. Prints of each individual were carried on field trips arranged in a dichotomous key for quick reference. After establishing that cow/calf groups were stable family units (Chapter 5), I rearranged the photo file to correspond to these groups. All elephants were given code numbers and the most commonly seen were named. Fig. 3.2 illustrates the range of appearance of individuals. A family unit book was used in conjunction with the photo file. The name, sex, estimated age, birth date when known, and individual characteristics of each animal were recorded in separate columns, on the same page as other members of its unit. Changes in ear outline or tusk breakages were sketched in this book, together with a summary of routine observations such as females in oestrous, disappearances of individuals, and other relevant events.

Modifications of this system (Douglas-Hamilton, 1967) have been used subsequently by Vesey-Fitzgerald. (1968), Hendrichs (1971), and Croze (in press), all of whom relied on sketches rather than photographs. Sketches are more convenient when few animals are filed as they are immediately available, but when differences are very small only photographs provide a sufficiently accurate record of finer details, and only photographs can instantly capture all the details of a shy elephant.

With practice I could also recognize a distinctive individuals from the air, and on many occasions I was able to identify and plot the positions of several family units during a short reconnaissance flight, immediately afterwards confirming my identification on the ground.

Coverage of Ground

A central position in the Park, overlooking the Ndala River, where the elephants frequently came to drink was selected as a base for research. The camp itself often served as a good observation point (Fig.

Figure 3.3 and 3.4

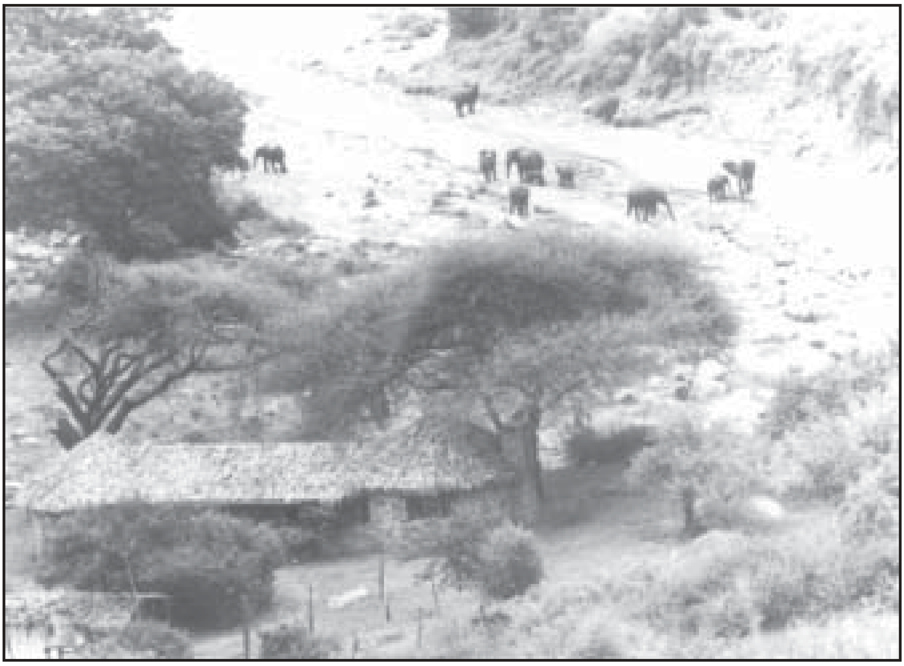


Fig 3.3: Ndala River Camp, base for the research project.

Fig 3.4: Two unrelated F.U.'s intermingle while drinking water below camp. The leading female, Mary, is aware of the observer's presence but pays little attention.

3.3). Apart from short interruptions when I had to be away, I patrolled various areas of the Park almost daily, in a landrover or on foot, for four and a half years trying to identify elephants whenever I met them. The patrols were organised to give as complete a coverage as possible, and I entered most parts of the Park every month. The patrols were not randomized samples, as any random system, while useful for estimating numbers and densities with known confidence limits, would impose an inflexible route and time schedule, which would not allow for unplanned deviations should conditions be favourable to stay with one group and follow it around.

I tended to go to areas where I knew I would find elephants. On encountering a group I would record the time, location, and general activity. Then on some days I would spend a long time attempting to identify every single individual in the group. These data first showed me that the cow/calf groups were stable family units (Chapter 6), and this stability allowed me to record all births and deaths within each group by registering the arrival of newborn calves and disappearances of individuals (Chapter 8). For this purpose on some days I followed groups until I could obtain an exact count. This often demanded a high degree of mobility on the part of the observer. Many observations were made from trees in areas where the vehicle was unable to penetrate or where disturbance had to be avoided. Confusion was increased by young males on the verge of puberty, which tended to drift away from their group (Chapter 5) and might remain unidentified for several hours if the vegetation was thick. The temperament of the elephants also greatly affected the ease of observation. Many groups were unapproachable, and would charge or run away on hearing the landrover engine. Most of the elephants were seriously disturbed by the presence of a vehicle when I first arrived. Gradually most of them habituated, and by the end of the study some individuals would tolerate the vehicle nearby, or myself on foot, without paying much attention to either (Fig. 3.4).

On other days I would range as widely as possible around the Park, preferably immediately following an aerial reconnaissance, in order to identify as many individuals and groups as possible to provide data on inter–individual and inter–group associations and spacing (Chapter 5 and 6).

Radio tracking

The visibility difficulties of Manyara made radio tracking a useful supplementary technique, particularly for recording daily and monthly movements, and for checking the accuracy of range maps made from discrete sightings on daily patrols. Many areas particularly in the South of the Park were so thick that it was virtually impossible to follow individual elephants in any other way. Radio tracking large mammals is a well tried technique, particularly in the U.S.A. (Craighead & Craighead, 1963), but elephants pose special problems. Transmitters attached to collars have twice been tried on elephants previous to this study (Laws, in wing &

Figure 3.5

A. **Radio tracking from the air along the Manyara Rift Wall. Note Yagi antenna tied to the struts. (Photograph by courtesy of Simon Trevor)**

B. **Bull elephant with newly fitted radio collar.**

Buss, 1970), but the collars broke, one after two days, the other after three weeks.

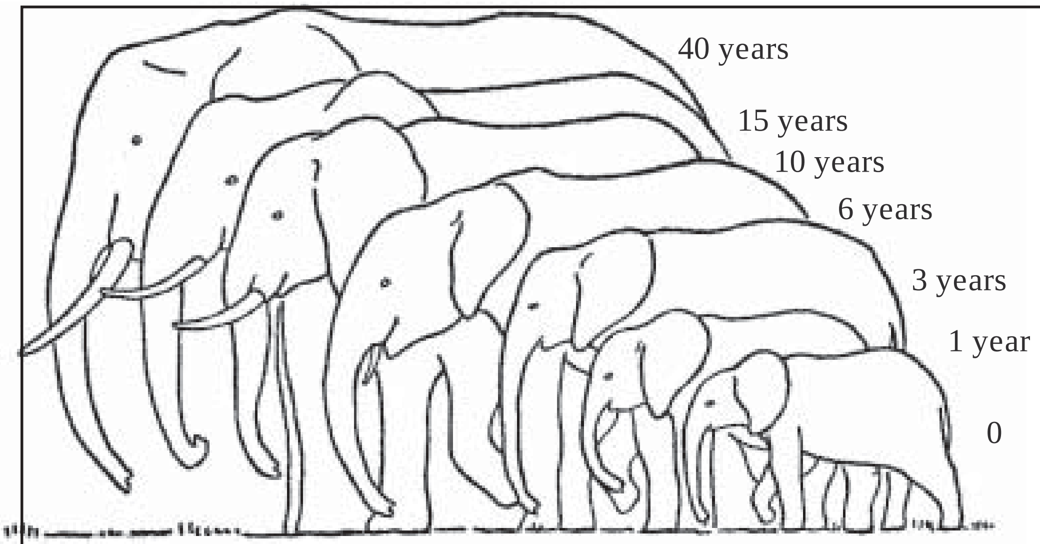
The equipment for Manyara was designed and assembled by Dr. Howard Baldwin of Sensory System Laboratories, Tucson, Arizona (Baldwin, 1971), to withstand the extreme strains that it might encounter if an elephant rubbed against a tree or if the collar became snagged on a stump. Transmitter, antenna, and batteries were sealed in a thick moulded fibreglass case, attached to the elephant by a collar of machine belting and held upright by a counter weight (Fig. 3.5B). The receiver and directional Yagi antenna could be carried on foot, mounted on a high pole on a car, or tied with cord to the struts of an aeroplane (Fig. 3.5A). These methods ensured maximum operational flexibility. The transmitters initially gave a range of about 50 Km. (30 miles) which slowly dropped off and two lasted for up to four months. The first elephant to be radio tracked at Manyara was immobilized by Dr. A. Harthoorn with Oripavine hydrochloride (M.99 Reckitt & Colman). I later used this drug following the dosage rates of Pienaar (1966). As the technique is not new I will not describe it further.

Age stimation

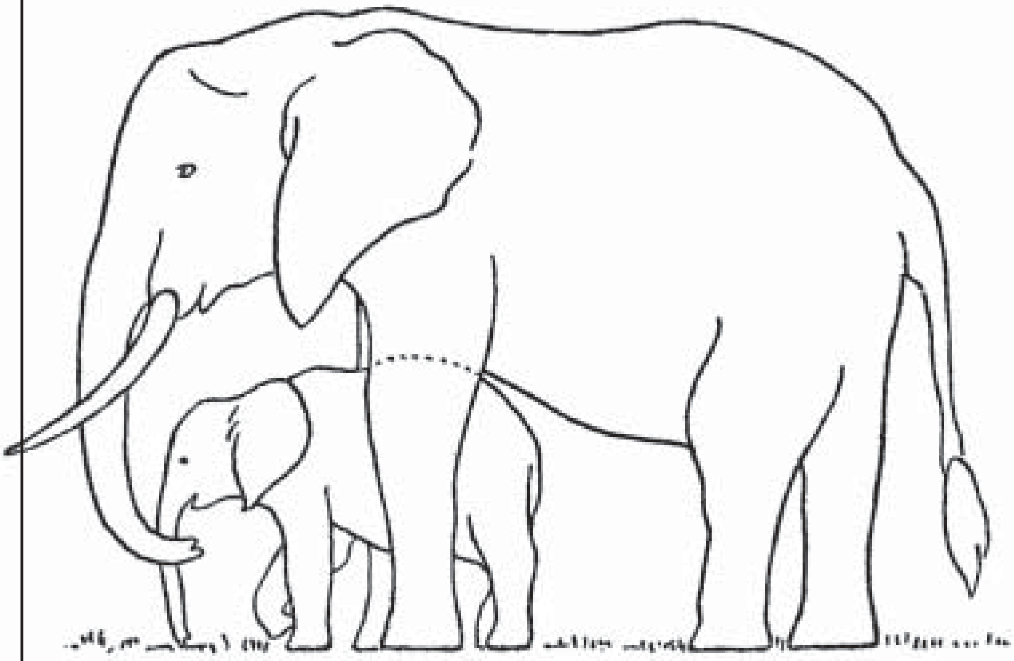
A number of systems have been developed for ageing elephants from the degree of tooth eruption and wear, upon which growth curves nave been based (Johnson & Buss, 1965; Laws, 1966 and 1970; Krumrey & Buss, 1968; Sikes, 1966, 1967, 1968c, 1971). The systems show little agreement in the ages which are more or less arbitrarily allocated to the various tooth categories. Laws had the largest sample of lower jaws with 793 in his collection, compared to Johnson and Buss n = 58, and Sikes n = 31. The only known age animal to be used as a check was 27 years old at death, and by Laws' system was estimated at 28 ± one year (Laws, 1969a). The large sample size and one empirical test suggest that Laws' system is probably the most accurate. After fitting a Von Bertalanffy (1938) growth curve to measurements of shoulder height at age, Laws (1966) constructed diagrams of elephant heights at different ages, which could be used as a field ageing guide up to fifteen years (Fig. 3.6). I adopted this system without modification for the Manyara population, assuming that possible local differences in growth rate would not seriously affect age estimations.

Subsequent work by Laws & Parker (1968) Laws (1969b, 1970) in Uganda and Kenya and flanks (1971) in Zambia, has shown that variations in growth rate are relatively small between populations and insufficient to cause serious errors in estimates of the early age groups. No confidence limits to the curves have been published, but the scatter (Hanks, 1971) appears small enough in the younger age groups up to the age of 15 to allow estimation to the nearest year. Much of the scatter may be an artefact of the rather approximate method of measurement, where the foreleg was manipulated until it looked straight; and the measurement taken with a tape from the edge of the sole of the foot to the crest of the scapula. The point corresponding to the scapula was

Figure 3.6
Age criteria for the African elephant (after Laws, 1966).



(1) **Shoulder height of female young in relation to adult cow.**



(2) **Size of calf at one year in relation to mother.**

fixed by sighting on the two scapulae so as to bring their dorsal edges into line (Laws, 1965, 1966). This scapula line might affect the measured height by several centimetres depending on how the elephant's fall affected the position of the two scapulae. While this variation may not seriously affect the calculated growth curve it might widen the confidence limits more than otherwise.

There is also the possibility that heights measured on a recumbent animal will be longer than on a standing animal when the joints are more compressed. However, flanks (1971) presents data from ten captive Indian animals showing that when recumbent they showed a mean increase of less than 1 per cent over the standing shoulder height, an error so small as to be negligible.

The field ageing system (Laws, 1966) depended on estimating the shoulder height of young animals as a ratio of the height of a fully grown cow. Some of these ratios I measured from photographs when cows and calves were standing very close together. As a further check on the accuracy of my subjective estimates I experimented in developing photogrammetric systems for measuring the shoulder heights accurately. These systems could only be used when, the top of the elephant's shoulder blade and sole of its forefoot were both visible and vertically aligned.

For a period I attempted to use a range finder and camera simultaneously; for as photographic image height is a function of focal length and range, the image height of an elephant could be used to calculate its true height if the range were known. This method was abandoned as simultaneous operation of camera and range finder was awkward and the 'Wild' range finder used was not sufficiently accurate for the purpose. Likewise a forester's dendrometer, normally used for measuring tree heights, proved to be very inaccurate.

A second method was to photograph an elephant, and then when it moved off to take a second photograph of a vertical scale held by an assistant on the exact spot where the elephant had stood a moment before. This allowed an accurate measurement of shoulder height. At 50 metres' range, displacement of the pole by one metre either towards or away from the camera only gave an error of 2 per cent, and I found this was a suitable range as the possibility of error was small enough to be acceptable and the elephant was close enough to allow its exact position to be located. (This method was also used by Foster (1966) on giraffe).

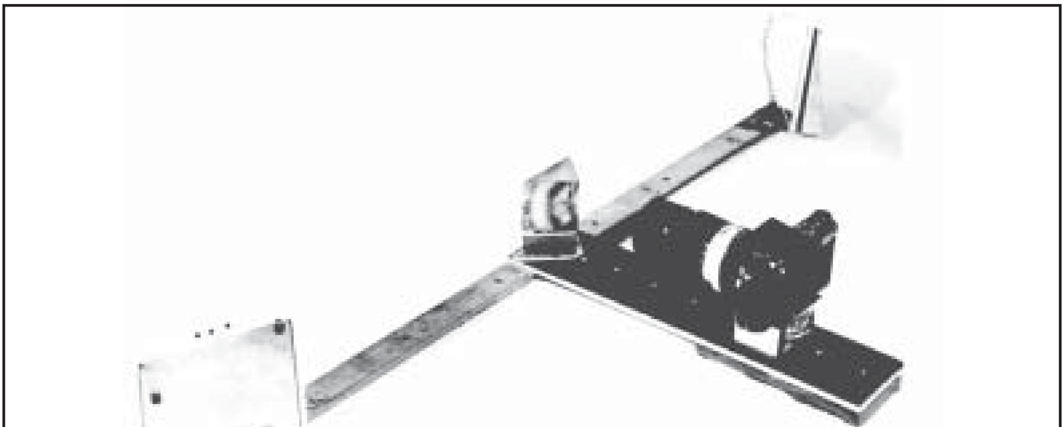
Unfortunately the method was time consuming. Although suitable for lone bulls, it was difficult to apply to the family units as the members were usually close together, the footprints, were difficult to distinguish, and they took a long time to move off. The forestry technique of measuring tree heights from aerial stereo-photographs made by twin cameras mounted at fixed distances apart on the fuselage, and operated. simultaneously (Mr. P. Williams pers. comm.), suggested to me the idea that elephant heights might be measured on the same principle. Finally I developed an attachment for the camera which took stereo pictures, each one of which contained information from which the true height of the elephant could be calculated. Although the principle of parallax forms the basis of most photogrammetry and is used in stereometric cameras and range-finders, the application described below is probably novel,

The Parallax Height Measurer

This device makes quick accurate measurements of elephants' shoulder heights at varying ranges. Essentially the apparatus is a 'T' shaped bar with a camera mounted on it as in Fig. 3.7. A 90^0 Prism, with front silvered faces, is mounted, immediately in front of the camera, with the apex of the prism perpendicular to the optical axis of the lense. A further pair of mirrors are mounted vertically, one on each end of the 'T' bar, separated by one metre and adjusted so that light rays, from an object on the optical axis of the lens, are reflected onto the two faces of the prism, and from the prism into the camera lens. This apparatus when properly adjusted splits the light rays coming from the object and focusses them in twin images on the negative. Fig. 3.8 illustrates the paths of light rays diagramatically. The two pictures may overlap slightly, but their separation may be sharpened by reducing the aperture to f8, and by moving the camera away from the prism. The apparatus can be used in conjunction with lenses of different focal length, and in practice I used a Nikon 35 mm. reflex camera with a 135 or 300 mm. lens.

The apparatus was light and easy to use in the field, (Fig. 3.9). Twin images of an elephant taken through the apparatus, appear in Fig. 3.10. The distance by which the images are separated (S), and the image height of the elephant (E) are both functions of range. Moreover, there is a

Figure 3.7 Photographic height measuring apparatus.



linear relationship between image height and image separation, at different ranges, which remains constant for any setting of the mirrors (see below). By calibrating the apparatus with objects of known height at different ranges it is possible to calculate the height of any object perpendicular to the axis of the camera.

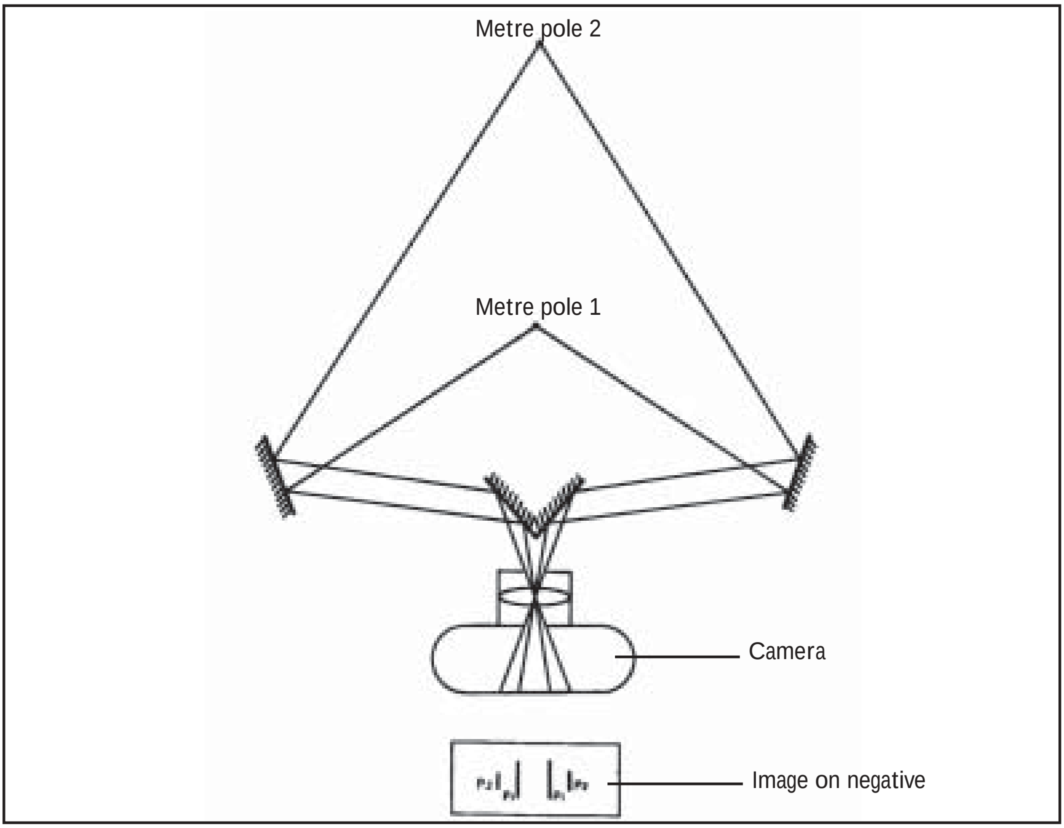
The method of calibration is as follows. Vertical poles, with a one-metre scale marked on each, are aligned, at varying ranges on the optical axis of the camera, and one or more photographs are taken. An example of a calibration photograph of such a line of poles appears in Fig. 3.11. Each pole has a twin image and the further metre scales on each pole have a smaller image height (M), and a wider image separation (S), than the nearer ones. Calculation, of a regression line of M on S, provides the image height of a one metre scale (M) for any value of image separation (S).

Expressed mathematically;

$$M = a S + b,$$

where a is the regression coefficient, S is the image separation and b is the intercept. The elephant's true height now has the same ratio to one metre as the elephant's image height (E) to one metre's image height (M); provided both E and M have the same image separation (S).

Figure 3.8 Pathway of light rays from two poles to the negative.



Mathematically this may be expressed as:-

$$\text{Elephant's True } \frac{\text{Height}}{1} = \frac{E}{M}$$

The elephant's true height can therefore be calculated from the regression formula by substituting for M:

$$\text{Elephant's True Height} = \frac{E}{a\,S + b}$$

In practice, calibrations were made by taking several pictures of the poles at, varying ranges and combining the measurements in one regression line. Fig. 3.12 is an example.

The measurements on the negative were made semi-automatically by recording the end co-ordinates of the distances to be measured, using a "bubble chamber track analysis measuring machine" in the Nuclear Physics Department of Oxford. This "medium precision" instrument designed by Vanguard, enlarged negatives 25 times, projecting them on a screen with a central cross-hair. The negative was mounted on a movable platform (platen), and any point on the negative image could be brought into position directly under the cross-hair by micro-manipulating servo-mechanisms. The co-ordinates of the point on the negative could then be recorded automatically, on paper tape to the nearest 2 microns. This equipment greatly increased the speed and accuracy of measurement, and stored the data in a form readily available for computer analysis.

Height measuring technique

Fig 3.9: Waiting for clear view of shoulder and feet before photomeasuring.

Fig 3.10: Double image of adult cow with appropriate coordinates and measurements. (see text)

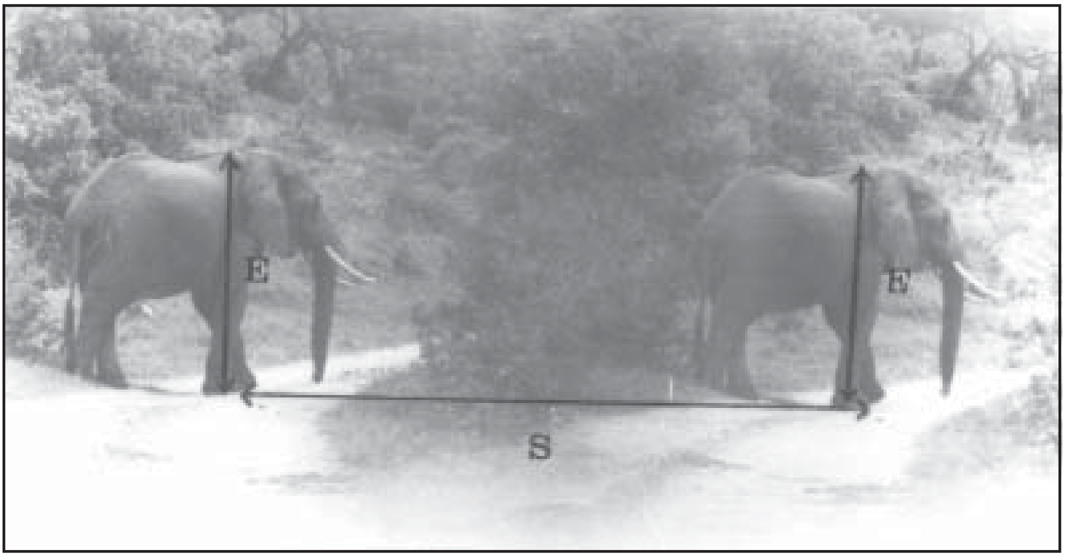


Fig 3.11: Double image of meter scales with appropriate coordinates and measurements. (see text)

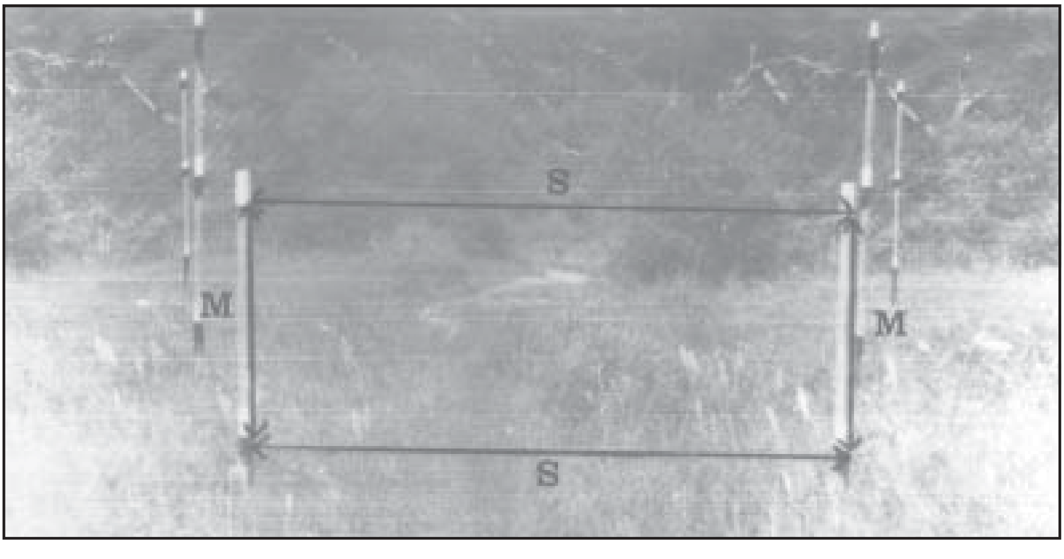
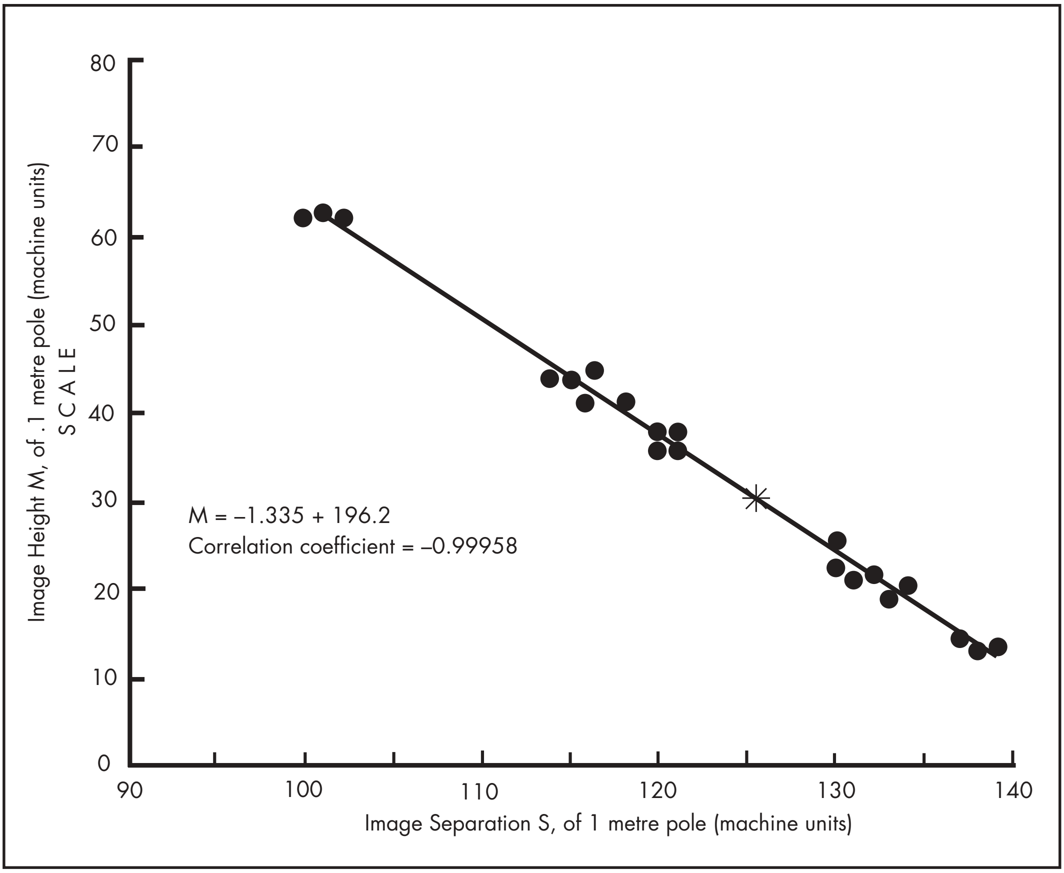


Figure 3.12 Calibration of parallax measure



Photogrammetric errors

There are a number of errors to which this technique is theoretically liable. The effect of each of these was minimized as follows, before testing the accuracy empirically.

Focusing error was caused by a change in magnification every time the focus was altered. This could be avoided by keeping the focus at infinity and relying on an adequate depth of field. (It would have been even better to fix the focus to cover the range of 30 – 80 metres).

Radial scale error is a property of every lens. If a scale with equidistant points is photographed at right angles to the optical axis of the lens, so that the scale image passes through the principal point of the negative, it will be found these points will not be separated by equal distances on the negative, and the error increases towards the edge of the frame. This error decreases as the focal length increases, and by using long lenses, for example 135 mm. and 300 mm. focal lengths, and by framing calibration and elephant measuring photographs so that they were restricted to the central portion of the negative this error was minimized.

Mirror error occurred when the mirrors were not properly adjusted. The pole images would appear to be out of parallel or at different levels. This was avoided by careful adjustment of the mirrors, while looking through the view finder, until the differences were undetectable. Great care was taken not to move the mirrors once they were set. Even a slight accidental shift would alter the intercept of the calibration regression line (Mo), making the calculated heights meaningless. As a check the apparatus was calibrated both before and after each field trip.

Tilt error would occur if the object to be measured were not perpendicular to the axis of the lens, for example if the elephant were on a slope, or when the lens were at an oblique angle. This was avoided by measuring only on flat ground when the elephant was standing upright, and never from above the level of the elephant's shoulder blade.

Close range errors were caused by large variations in image separation and image height at short distances. A point selected on the shoulder blade of an elephant at 15metres might have a different image separation value to that of the foot. Also the sole of the foot might appear curved giving no clear level to select for measurement of height. These errors were avoided by making no measurements at less than 30 metres distance.

Long range errors were caused by; difficulties in interpreting very small images on the negative. A slight measurement error would cause a large percentage error in the calculated height of an elephant. The increase in magnification afforded by the 300 lens reduced this error, but it was more practical to use the 135 mm., with its greater depth of field and. to restrict measurements to distances of less than 80 metres from the camera. A camera with a larger format would also improve image measurement accuracy.

Accuracy testing

A general correction was made which reduced many of the above errors. Four co–ordinates were plotted, during calibration (see Fig. 3.11), from which two S values and two M values were calculated and averaged. Six co–ordinates were plotted for each double elephant image (see Fig. 3.10), from which two E values were averaged and one S value was measured.

The value of this parallax device depended on its accuracy, which could be tested empirically by measuring objects of known height. 26 poles of known height were tested in this way. The mean deviation of photo-height from true height was 3.2 cm. and the 95 per cent confidence limits were ± 8 cm. The deviation was related to range and appeared to be caused by the difficulty in interpreting small image at long range. In practice I avoided long distance photographs of elephants and restricted measurements to ranges of 30–80 metres. The empirically determined accuracy of the apparatus within these range limits greatly improved, with a mean deviation of 2 cm. and 95 percent confidence limits of ± 5.7 cm.

A further test was to compare separate measurements of the same elephant. Out of 19 elephants measured twice, the mean difference in measurements was 4.2 cm. with a range of 0–16 cm., the larger deviations again occurring at long ranges.

With further refinements in calibration it may be possible to narrow the confidence limits of measurement. This device could have applications in many fields of research where quick accurate estimations of height need to be made at a distance, and at present is probably the most accurate method of measuring elephant shoulder heights.

Unfortunately a working prototype of the apparatus was only developed late in the study, after several experimental models, and during 1970 it was possible to measure only 108 individuals of the sample of 28 family units which totalled 302 members in mid-1970. However the method provided a check on subjective age estimations, and up to the age of 15 there was usually agreement to within one year.

The ages of calves that were born during the study period were mostly known to within the nearest month and the estimated age structure up to the age of five years is therefore accurate. Thus the inaccuracy caused by the poor fit of the Von Bertalanffy equation below the age of five years (Laws & Parker, l968) was avoided. Animals up to 8 years old in l970 were probably estimated within the correct year age class, as they were only four years old at most when first estimated in 1966, and it is relatively easy to assign year classes to animals under five years, when the differences between one year and the next are marked due to rapid growth. From 8 to 12, the estimates are probably accurate to within one year, from 12 to 15 to within 2 years. Estimates of known animals made early in the study were usually compared with later estimates of the same animals as a check. Another check was provided by the shoulder height rank order observed within each family and between animals of different families when these intermingled.

Adult females above the age of 15 were at first divided into 5 subjective size categories, based on body and tusk size. This was done largely by comparing animals when they stood together. Later, when it became possible to measure shoulder height accuracy, I re-arranged the adult size categories 1 and 2, to correspond roughly to 15–20, and 21–30 year age classes. The variation in shoulder height beyond the age of 30 years precludes age estimation based on this parameter, but I continued to rank them according to size.

CHAPTER 4 — NUMBERS AND DENSITY

Visibility of elephant from the air.

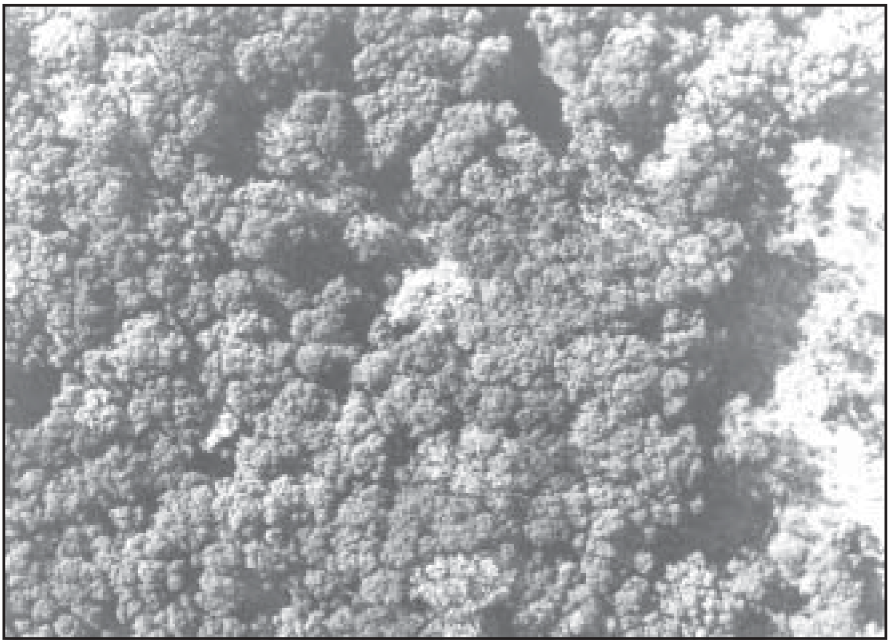


Fig 4.1: Closed canopy in the Northern forest made aerial counting difficult.

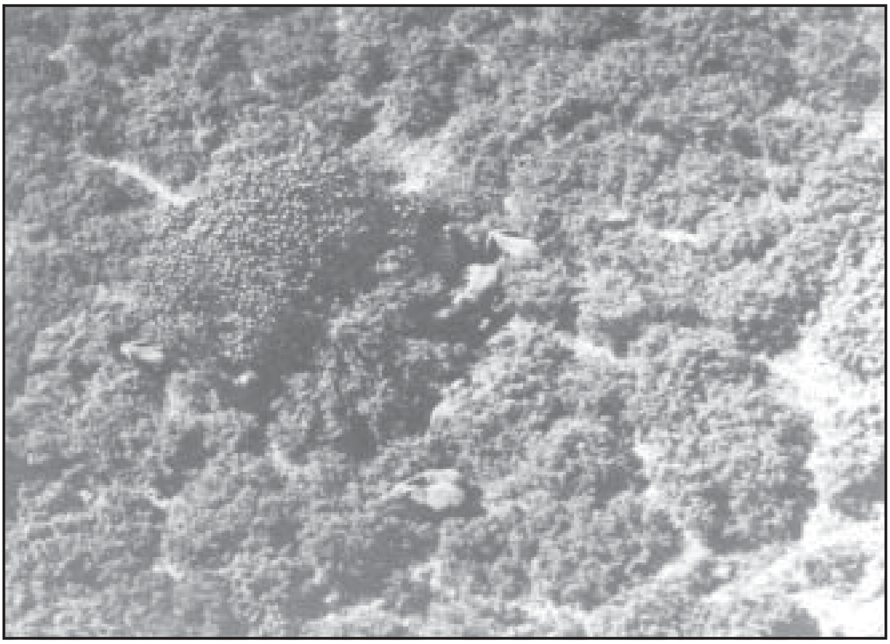


Fig 4.2: Tall thickets and trees partially concealed elephant groups in the Endbash area to the South.

NUMBERS AND DENSITY

In 1961 Mr. M. Morgan-Davies, the first Warden of the National Park estimated the elephant population to be 400, from his routine ground patrols. The first aerial count of Watson & Turner (1965) totaled 420 elephants, which indicated that the density of elephants in the Lake Manyara National Park exceeded that of any other area known in Africa at that time. It remained to be established whether this density was consistently high around the year, and how it was distributed among the various habitats. Both aerial and ground censuses were made in this study. The ground counts relied on a method of individual registration and, as they were believed to be more accurate, were used to correct the aerial counts.

Aerial Counts

Aerial counting is not straightforward. Lamprey et. al. (1967) demonstrated that even in open country the size of elephant groups counted by eye from the air tend to be consistently underestimated, when they compared visual estimates with counts made from aerial photographs taken at the same time, in the Serengeti. At Manyara even in relatively open areas too many of the groups were hidden under trees for photography to be successful (see Fig. 4.2). 17 per cent of the Park was forest, with a closed canopy in places, concealing an unknown proportion of elephants, which Watson & Turner (1965) had arbitrarily considered to be up to 10 per cent in their count (see Fig. 4.1). On sunny days many more elephants were hidden in the shade of trees than when the sky was overcast; also certain groups responded to the aircraft by rushing into the forest, while others paid no attention.

Further factors affecting the number of animals counted, were the observer's and pilot's experience. A pilot unfamiliar with the area could not fly accurately or locate himself, and a new observer tended to miss groups. Visibility also varied; a soft light with moderate contrast was better than direct sunlight. The amount of leaves on the trees affected visibility, which improved in the dry season when the leaves of many species fell or withered. Despite all these variables aerial census was the only method of counting large areas quickly.

In all 15 total counts were made of the whole Park. Several flight patterns were used, including the transverse pattern of Watson & Turner (1965) as well as longitudinal flight patterns and inward spiralling around small well defined blocks. The Park was small enough to allow a thorough coverage and whenever a group was encountered it was circled until a consistent count was obtained, and its position was marked on a l : 50,000 map.

Table 4.1:

Total aerial counts of elephant: Lake Manyara National Park.

		Number Counted	Corrected Value (Increased by 27%)	Pilot	Observer
1965	Apr.	420	–	Turner	Watson
1966	26 Feb.	226*	–	Palfrey	I. D–H
	20 Mar.	I98*	–	Turner	Bell
	21 Mar.	235*	–	Turner	I. D–H
	15 Jul.	199*	–	Field	I. D–H
	22 Oct.	290*	–	Turner	“
1967	19 Jan.	320	406		“
	17 May	315	400	Lamprey	“
	20 Aug.	272*	–	Lamprey	“
1968	14 Apr.	148*	–	Field	“
	29 May	331	422	Lamprey	“
1969	7 Mar.	340	504 (48%) •	I. D-H.	Olivier
	7 May	374	475	“	Sinclair
	25 Jul.	299*	380	“	Olivier
	17 Dec.	318	402	“	Burengo
1970	22 Mar.	203 *	–	“	Burengo
	Mean	280	427		

* **Counts in which conditions were poor because of one or more of the following factors: bad weather, insufficient light, elephants standing under trees in heat of the day, pilot or observer inexperience. Other aerial counts were made under conditions, but must be considered as minimum estimates for which appear in the text (see opposite page).**

• **Corrected Total calculated separately for North and South, see text.**

The results of all aerial counts appear in Table 4.1.

Correction of Aerial Counts

As a rule it was not possible to compare total aerial and ground counts made simultaneously. However, on the 7th March l969 a detailed aerial census of the whole Park, made under good conditions, coincided with a thorough ground coverage made at approximately the same time. The total counted from the air came to 340 elephants. From the Bagayo Narrows to the north end of the Park, the total was 164, and this sub-area on the same day was caused by ground registration revealing 15 known family units and 10 bulls which numbered 178 exactly. This method relied on knowing the exact numbers in each family unit identified. Within one day on either side of the aerial census five more family units, numbering 69 animals, were identified in this area, all at least 7 Km. north of Bagayo Narrows, which suggests that they had not just moved in but had been overlooked. Three more family units, none of which were ever seen out of the northern section (Chapter *5)*, were identified within five days of the aerial census, adding a further 29 animals to the total. Table 4.2 below compares the aerial count with the figures derived from registration:

Table 4.2: Numbers in the North Half of the Park

	NUMBER	DEVIATION	% DEVIATION
Counted by air 7th March, l969	164	0	0
Registered on ground: same day	178	14	8.5%
Registered 5th/6th March	247	83	50%
Registered 2nd/9th March	276	112	68%

I conclude that these results show that the northern aerial count needed to be increased by 68 per cent to give the true total. However the visibility in the south was somewhat better and a lower correction factor was necessary, which could be calculated from a number of ground comparisons as follows:

92 reconnaissance flights were flown between January l969 and July 1970. The main objective of these shorter flights was to plot seasonal distribution (see below), but in some, a complete count of a small well defined block could be compared with exact ground counts of the same block, made within minutes of landing. Out of 39 small blocks counted by air 11 tallied exactly with the ground counts, but in areas of thick canopy the aerial count was as much as 88 per cent below the ground estimate. The median underestimate was 20–25 per cent. (Appendix 1). In other words the aerial counts needed to be increased by about 25–30 per cent. Ideally a separate correction factor should have been made for each visibility type, but in practice these checks only applied to the semi-open Acacia tortilis woodland and escarpment zones. However visibility from the air is not greatly different in the South and it is probably justifiable to increase the number in the South counted on 7th March l969 by 27 per cent, the median correction value. Thus the total value for the South was increased to 224, and the total for the North, by the previous correction of 68 per cent, was increased to 276, making a grand total of 504.

The 27 per cent correction Value was also applied to other counts, made under good conditions. Since it was calculated from counts in relatively open areas it was probably still too low for the forest areas and so produced minimum corrected estimates. After excluding counts which were believed to be low due to adverse factors, seven counts remained, (excluding that of Watson & Turner, 1965), with a mean corrected value of 427 (Table 4.1).

Similar tests of the accuracy of aerial counts of elephants have not been made in other studies, but underestimates of a similar order might be expected in areas of comparable visibility. Goddard using a similar method, obtained a correction factor for rhino in the Olduvai gorge, and applied it to census data in Tsavo increasing numbers by 200–700 per cent (Goddard, 1969). In comparison the correction factor of 27 per cent for the Manyara elephants in an area of poorer visibility than Olduvai appears conservative, even though clumped elephants are easier to spot than solitary rhino.

Registration Census

The number of family units observed also gave an indication of overall movements into or out of the Park and could be used to calculate the minimum number of elephants using the Park over a period, such as a quarter of a year.

From January 1966 to January 1968 l identified 47 separate family units. The number of new groups encountered per quarter is illustrated in Fig. 4.3 and shows a rapid initial fall–off in the first year. By

March 1968 I was probably familiar with every cow/calf group using the Park. For the next one and three quarter years I saw no new groups until December l969, when I encountered SPL F.U. for the first time in the southern Endabash delta of the Park; a very distinctive group with a large splay–tusked matriarch. This group had moved down from the Marang Forest where I had previously seen them in September 1969. They may have been entering the Park for the first time as I am convinced that I would not have missed them had they frequently appeared in the park before.

Figure 4.3

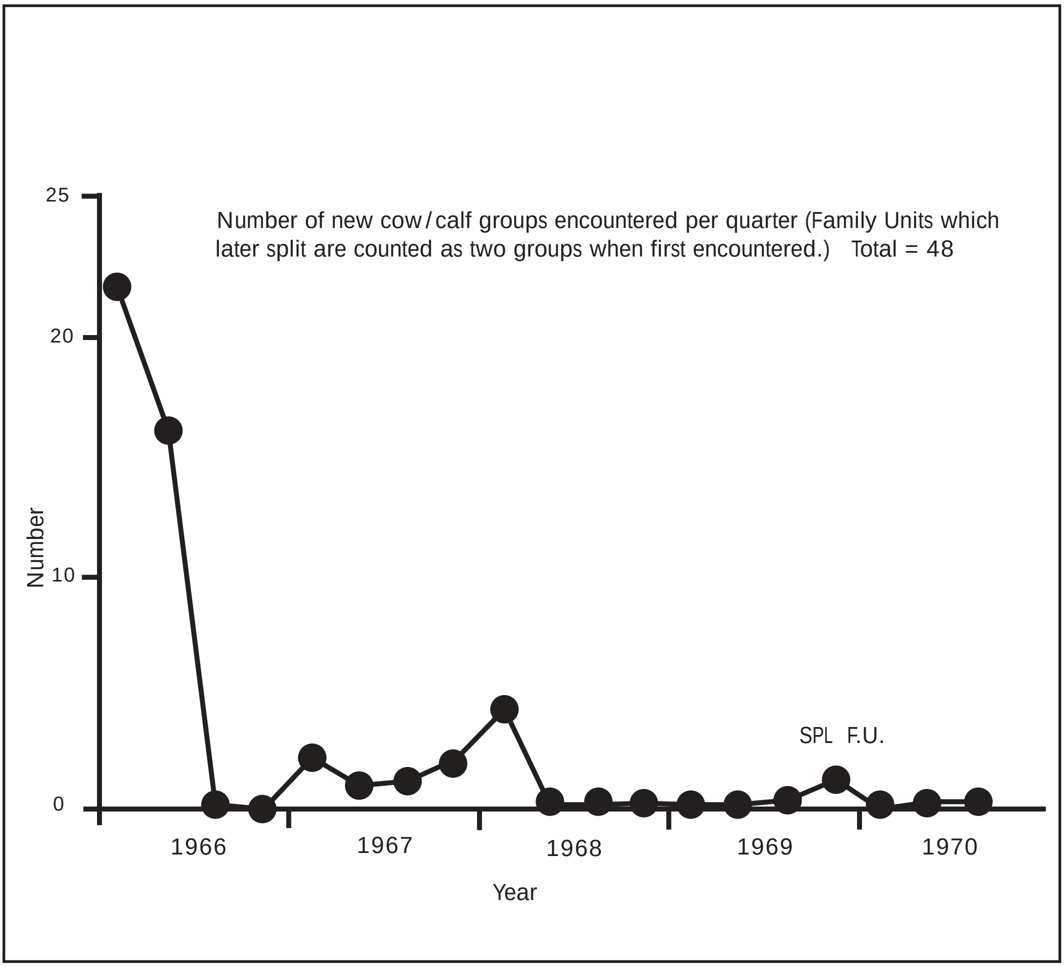
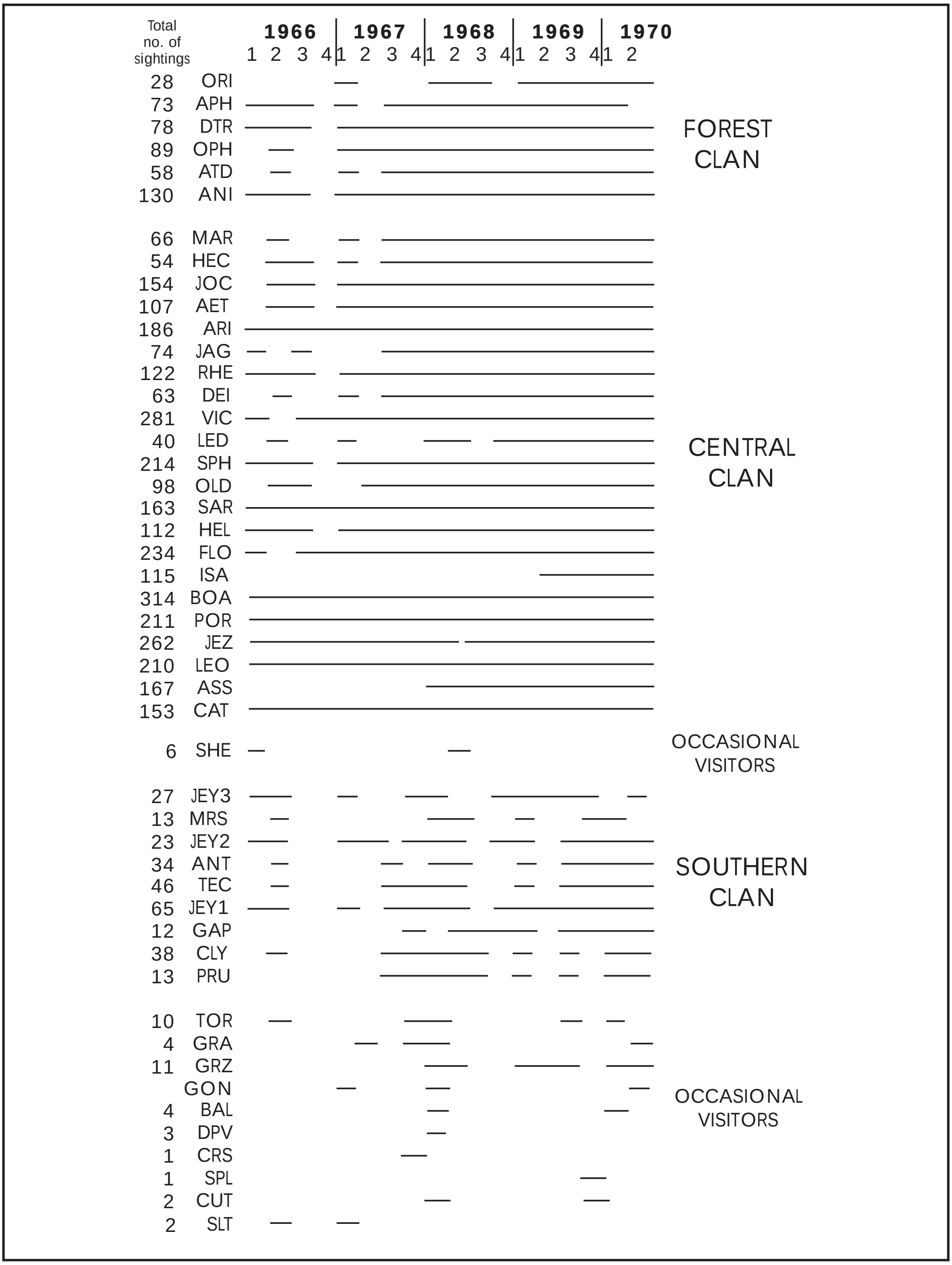


Figure 4.4
Quartely sightings of family units.



A horizontal line indicates that a family unit was seen within a quarter.

The number of new bulls encountered per year did not fall off. 47 new bulls were seen in 1966, 16 in 1967 and 22 in 1968. Only 16 bulls were seen throughout the three years. This was partly because bulls, being either single or in small groups (see next chapter) were harder to see than cow/calf groups, but these figures also suggest that tile bull population was much more transient than the cows and calves. After 1968 the task of keeping a close record of all bulls which entered or left the Park was beyond the scope of this study, and the number of bulls in 1969 and 1970 was estimated from the mean ratio of the previous three years.

Fig. 4.4 illustrates family unit sightings by quarters over four and a half years. I have chosen the quarter as a unit since during each of these periods I covered most of the Park. A horizontal line indicates that a family was seen in the appropriate quarter.

To calculate the number of elephants using the Park, the following assumptions were made:

(1) That one animal of a family unit implied the presence of the rest of its unit in the immediate area. (See Ch.5).

(2) That the yearly mean group size of a sample of about 56 per cent of all family units (Ch. 5,`) could .be applied to the remainder. Mean group sizes and standard errors appear in Table 4.3 below.

The estimates were obtained by the formula,

N = (No. F.Us x Means size) + bulls

As some of the units seen in a year were not permanent residents the numbers present at any one time would be less than

Table 4.3: Yearly population determined by registration.

	1966	1967	1968	1969	Half 1970	1966-1970
No. F.Us seen	35	39	44	41	42	48
Mean F.U. Size ± s.e.	10.4	10.4 ± 0.88	11.0 ± 0.88	10.8 ± 0.1	10.8 ± 0.96	10.7
Cow/calf Nos. (Mean x No. FUs)	364	406	484	443	454	514
Bulls seen	47	42	46	(47)	(49)	80
Bull % ratio	12.6	10.3	9.5	(10.7)	(10.7)	15.5
Population total	411	448	510	480	503	594

the yearly total. If it is assumed on the basis of regular sightings and range maps (see Ch. 5): that certain family units never left the Park even though they may occasionally have been overlooked for more than three months, then numbers fluctuated above a basic level depending on the visits of groups and bulls which were not wholly resident, and can be estimated for each quarter.

Even if this rule were occasionally broken by one of the 'resident' F.Us leaving the Park, the gap left in the total by its absence would probably be more than compensated for by the presence of groups which I had missed on the ground in the Endabash thickets. The ratio of bulls to cows and calves was also uncertain as although the mean yearly ratio between 1966 and 1968 was 10.7:100, the ratio over the whole period of all bulls seen in total to all the members of family units seen in total was 15.5:100. These factors allow minimum and maximum population estimates to be calculated for every quarter.

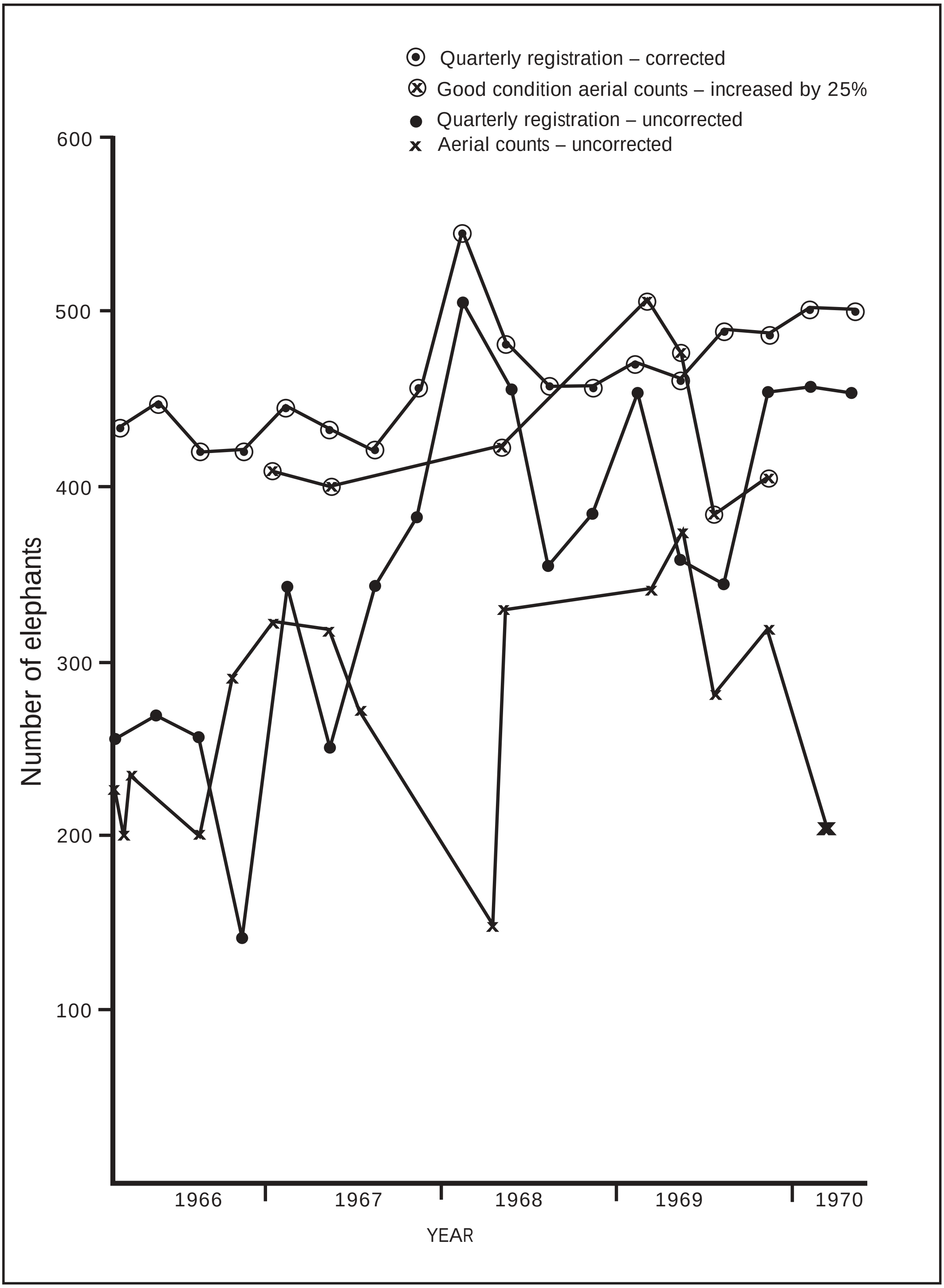
In Fig. 4.5 ground and aerial estimates are plotted together, with both minimum and maximum values for each. The successive estimates all show a trend towards increase. Exactly the same sort of apparent increase in total aerial counts has been recorded for elephants by Pienaar (1966) and by Field (1971). Watson & Bell (1968) record an increasing probability of sighting elephant on reconnaissance flights made in the Serengeti between 1962 and 1965. All these authors attribute the increases to elephant immigration into their areas, but unfortunately it is impossible to assess the extent to which these increases may also be due to the observers' and pilots' increasing skill and knowledge of their areas. The large increases in the uncorrected aerial and ground estimates at Manyara may mainly be attributed to my increasing knowledge of the area and the elephants, rather than to immigration. This interpretation is supported by the relatively high number recorded in the same area before my study period by an experienced pilot and observer (Watson & Turner, 1965). (Table 4.1).

However, the corrected registration results show a gradual increase of approximately 3.5 per cent annually which I attribute mainly to recruitment, which will be further described in Chapter 8. Only the entry of SPL F.U. was suggestive of immigration and I conclude that any major build up in numbers probably occurred before my study period. However, future immigration could be greatly increased if the Marang Forest lost its protected status.

No obvious seasonal trends emerge from the quarterly registration, as the troughs in numbers observed in late 1966, 1967 and 1968 coincided with periods when I was away for part of the quarter. The mean population values over 4 $^{1}/_{2}$ years were as follows:-

Number	Mean Total
16 Uncorrected aerial counts	280 (made in all conditions)
8 Corrected aerial counts	427 (made under good conditions only)
14 Minimum quarterly registrations	374
14 Corrected quarterly registrations	462

Figure 4.5
Census results by air and ground estimation.



I conclude that numbers within the Park probably fluctuate between 400 and 550, and that should all the temporary visitors be forced into the Park, the population would rise to a minimum 594 elephants. The mean corrected aerial count of 427, which I regard as a conservative estimate, gives an overall density for the Park of 5 elephants per square kilometre. The mean corrected registration estimate of 462 is probably more realistic and gives an overall density of 5.5 elephants per square kilometre (13–14 E/sq. ml.).

Seasonal Chances in Distribution

Seasonal changes in distribution could be measured by reconnaissance flights. 92 flights were made for various purposes, which included radio-tracking and administration. The area covered in each varied, and distribution could best be plotted by a variation of Watson's (1967) occupancy method.

For this purpose a fine grid of $^1/_4$ Km^2 squares was superimposed on the 1 : 50,000 map. After each flight the squares which had been searched and the number which contained elephants were tabulated. The Park was stratified into 8 areas which corresponded to the major habitat and visibility types (Fig. 4.6). In this way it was possible to estimate the population's distribution as a percentage of the squares covered which contained elephants, within each habitat and over each season.

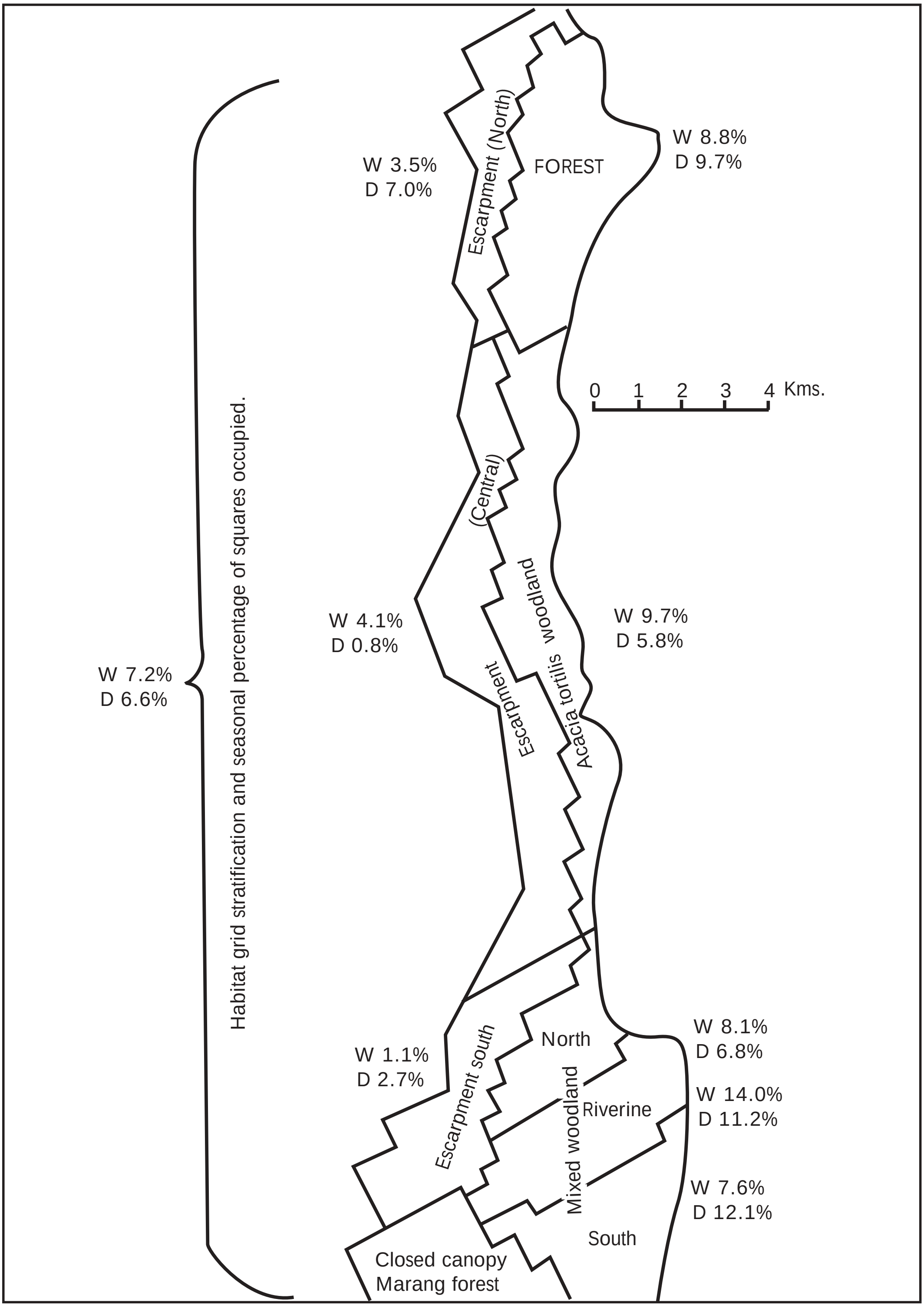
This measure of distribution was particularly suited to Manyara conditions as it was less affected by visibility differences between habitats than total counting. Although individuals in the forest were more likely to be overlooked than in the woodlands, it was less likely that an entire group in a $^1/_4$ kilometre square would be missed altogether.

This measure was also directly proportional to the density, since ground counts, air counts and group registration showed that there were no significant differences in group sizes or inter-group spacing in relation to seasons or ranges (Appendix 6.3–6.6).

As remarked before, the elephants' distribution was very clumped. Over the whole series of reconnaissance flights the elephant population on average occupied 7 per cent of the total area available. In other words the total population of some 450 elephants was usually found within grid squares which totaled 6.1 Km^2 in area.

The results were pooled for the wet and dry seasons of 1969 and 1970, and appear in Table 4.4. The dry season covers the months of June to October, all other months are classed as wet months (for justification see Fig. 2.2). The squares sampled within each area have been tabulated according to whether they contained or lacked elephants in the wet and dry season. The proportion containing elephants are presented as a percentage and seasonal differences are tested by a X^2 analysis with Yates' correction.

Figure 4.6



Escarpment (North)
FOREST
W 3.5%
D 7.0%
W 8.8%
D 9.7%
0 1 2 3 4 Kms.
(Central)
Acacia tortilis woodland
W 4.1%
D 0.8%
W 9.7%
D 5.8%
W 7.2%
D 6.6%
Habitat grid stratification and seasonal percentage of squares occupied.
Escarpment
Escarpment south
W 1.1%
D 2.7%
North
W 8.1%
D 6.8%
Mixed woodland
Riverine
W 14.0%
D 11.2%
W 7.6%
D 12.1%
South
Closed canopy
Marang forest

If the results for the whole Park are pooled, there is no significant difference between wet and dry seasons, (despite the heavy sampling bias in favour of the acacia woodlands which would tend to give a spurious significance to seasonal differences, see below). Thus I conclude that there are no large-scale movements in and out of the Park on a seasonal basis.

On the assumption that the mean number of squares occupied by elephants within a habitat is proportional to their numbers in that area, it was possible to calculate the relative density within each habitat. Absolute densities for each habitat have also been calculated from the population estimate of 427, derived from the mean corrected aerial count, and appear in Table 4.5.

The density in the Northern Forest was higher than in the acacia woodlands in the dry season, but lower in the wet season within habitats only the <u>Acacia tortilis</u> woodland and central escarpment were shown to have significant seasonal differences, at the .001 and .01 levels of probability respectively. This change in density was also very obvious from the ground patrols. At the time when the Acacia woodlands became drier and the mud wallows disappeared, the elephants made their way to the swamps and shade found in the North and in the South. From time to time they re-entered the Acacia woodlands throughout the dry season, particularly in July and August when the bulk of the <u>Acacia tortilis</u> seed crop, a favoured food of elephants (Chapter 7), was shed. None of the other habitat types showed significant differences between wet and dry distribution even when lumped together.

The escarpment zones had a lower density throughout the year than the habitats immediately below them. This could be attributed to three possible factors: that the elephants avoided the nearby Wambulu settlements; that the area had a low food availability, or that in the exposed sun they became too hot. The mainly nocturnal use of the escarpment (Chapter 5) suggests that the first and last explanations are plausible. The seasonal differences in density Table 4.5 suggest that food availability may explain their distribution. Probably all three factors play a part.

The density appeared to be higher all round the year in the Southern Endabash delta, than in the Northern zones. As food seemed to be no more abundant than in the North, other explanations must be sought. It is possible that following the displacement of elephants from the Magara farms, to the south of the Park some of these may have taken up residence in the South of the Park, thus increasing the density. Another possibility is that the elephant groups living mainly in the highly leached Marang Forest, probably needed to enter the Park at frequent intervals in order to eat enough salt, thus swelling the numbers in the South. The Wambulu tribesmen, who graze their cattle within the Marang Forest glades and around its fringes, feed their cattle a salt supplement once every two weeks, and elephants in the same area are probably unable to acquire enough by feeding in the forest alone. In the Wankie Game Reserve, Rhodesia, an area deficient

Table 4.4: Seasonal and habitat variations in relative density, calculated from 92 aerial reconnaissance flights (see text).

NO OF FLIGHTS: 49 DRY 43 WET	AREA $^1/_4$ KM^2 A	SEASON	SQS -E B	SQS +E C	X^2 FOR 1 DF.	PROBABILITY THAT SEASONAL DIFFERENCE IS DUE TO CHANCE	% SQUARES OCCUPIED D	MEAN NO. SQUARE OCCUPIED/ AREA E
SCARP (North)	29	DRY	132	10	1.90	> .1	7.0	2.0
		WET	274	10			3.5	1.0
FOREST	58	DRY	1102	119	.54	> .1	9.7	5.7
		WET	1107	91			7.6	4.5
SCARP (Central)	68	DRY	355	3	8.03	< .01	0.8	0.6
		WET	1002	43			4.1	2.8
ACACIA TORTILIS WOODLANDS	54	DRY	2624	158	28.6	< .001	5.8	3.1
		WET	2047	220			9.7	5.2
SCARP (South)	40	DRY	108	3	(Fisher's exact test)	> .1	2.7	1.1
		WET	159	3			1.9	0.74
MIXED WOODLAND (North)	23	DRY	737	54	0.68	> .1	6.8	1.6
		WET	553	49			8.1	1.9
(Riverine)	40	DRY	659	83	1.99	> .1	11.2	4.5
		WET	422	69			14.0	5.6
(South)	42	DRY	364	50	3.84	.05	12.1	5.1
		WET	350	29			7.7	3.2
TOTAL	354	DRY	6081	480	2.48	> .1	† 6.6	23.5
		WET	5855	514			† 7.2	25.40

KEY: $D = \frac{C}{(C+B)} \times 100$ $E = \frac{C}{(B+C)} \times A$ † $\frac{(\sum E)}{\sum A} \times 100$ i.e. % corrected for differential sampling.

Table 4.5 Seasonal and habitat variations in Absolute Density calculated from an assumed total of 427. (see text)

AREA $^1/_4$ km^2	A	SEASON	MEAN NO. SQUARES WITH ELEPHANTS E	% POPULATION PER HABITAT TYPE F	% POPULATION PER km^2 H	ELEPHANTS / km^2 TOTAL POPULATION = 427 I
SCARP (North)	29	DRY	2.0	8.8	1.0	5.2
		WET	1.0	3.9	0.5	2.3
FOREST	58	DRY	5.7	25.1	1.7	7.4
		WET	5.1	20.1	1.4	5.9
SCARP (Central)	68	DRY	0.6	2.6	0.2	0.7
		WET	2.8	11.0	0.6	2.8
Woodlands	54	DRY	3.1	13.7	1.0	4.3
		WET	5.3	20.9	1.5	6.6
SCARP (South)	40	DRY	0.1	0.4	0.04	0.2
		WET	0.5	2.0	0.2	0.8
Mixed woodlands (North	23	DRY	1.6	7.0	1.2	5.2
		WET	1.9	7.5	1.3	5.6
(Riverine)	45	DRY	4.5	19.8	1.8	7.5
		WET	5.6	22.0	2.0	8.4
(South)	42	DRY	5.1	22.5	2.1	9.1
		WET	3.2	12.6	1.2	5.1
Whole park	354	DRY TOTAL	22.7	100	1.21	5.2
		WET TOTAL	25.4			

KEY:

$$F = \frac{E \times 100}{\sum E} \qquad H = \frac{F \times 4}{A} \qquad I = \frac{H \times 427}{100}$$

in minerals, the sodium ion concentration in the few water pans available, may be the principal determinant of elephant density (Weir, 1972).

Discussion

Considering the thickness of the vegetation and the timidity of the southern elephant groups it is probable that the corrected aerial and ground estimates of total elephant numbers are still below the true value. However, the mean density of 5 elephants km^2 can safely be accepted as a minimum estimate of the elephant density around the year at Manyara.

No other area in Africa has been shown to have such a high overall elephant density. Appendix 10 lists elephant. census results, estimates and densities for elephants all over Africa. Many of these, however, may also be underestimated for the reasons discussed previously, but only two areas, that may reliably be compared, approach the year round elephant density of Manyara. They are the Murchison Falls Park South Bank, (M.F.P.S.) which in one stratum had a density of 3.8 E/km^2 (Laws, 1972) and the Queen Elizabeth National Park (Q.E.P.), with densities in some habitats of up to 3.5 E/km^2 (Field and Laws, 1970). Certain blocks of 10 Km^2 in M.F.P.S., had densities in excess of 10 E/Km^2 but this concentration probably moved around so that the density was evenly distributed within a larger stratum over the year (Laws, in press).

The large mammal biomass of the L.M.N.P. was also relatively high. The animal population of Lake Manyara had largely been cut off from the Masai steppes by rising Lake, and numbers tended to remain consistent, since there was little movement in and out of the Park of species other than elephants.

Buffalo, which numbered 1507 in Watson & Turner's count were recounted in May 1969 using the same photographic technique and numbered 1548, which suggests that their numbers had not changed significantly. Giraffe were censured by registration in 1968, and numbered 60. Impala counted on the ground numbered 451 (Makacha & Schaller, 1969). Rhinos counted from the air in 1963, 1969 and 1970 reached a maximum of 23. The major large animals living in the Park are summarized in Table 4.6, including Watson & Turner's (1965) estimates. A minimum number for waterbuck, bushbuck, baboons, reedbuck and hippo, relatively cryptic species not seen in the 1965 aerial census, has been arbitrarily estimated from the frequency with which I encountered them on patrols, and has been added to Watson & Turner's count and to my later estimates. Biomass conversions have been calculated using Field & Laws' (1970) unit weights for elephant, buffalo, hippopotamus, waterbuck, bushbuck and reedbuck, for the remaining species I have used Lamprey's (1964) adjusted averages (table 4.6).

It will be seen that the large mammal biomass was dominated by the two species, elephant and buffalo, which formed 49 percent and 42 percent of the biomass respectively.

Table 4.6:

Total biomass of large mamals in Lake Manyara National Park and biomass per hectare. Watson & Turner (1965) estimates have been corrected and recalculated.

	Kg. Unit weight	APRIL 1965 (Watson & Turner. 1965) Aerial Count			1966–1970 (Mean or Minimum Numbers)		
		Number	Biomass Kg.	% Biomass	Number	Biomass Kg.	% Biomass
Elephant (Loxodanta africana, Blumenbach)	1700	421	715,700	50.4	427	725,900	49.0
Biffalo (Syncercus caffer)	395	1507	595,265	41.9	1548	611,460	42.0
Hippopotamus (Hippopotamus amphibius, Linnaeus)	1000	10	10,000	0.7	10	10,000	0.7
Zebra (Equus burchelli)	246	115	28,290	2.0	75	18,450	1.2
Impala (Aepyceros mefampus, Lichenstein)	50	285	14,250	1.0	451	22,550	1.5
Rhinoceros (Diceros bicornis, Linnaeus)	982	20	19,640	1.4	23	22,586	1.5
Giraffe (Giraffa camelopardalis, Linnaeus)	759	31	23,529	1.7	60	45,540	3.1
Wildebeeste (Connochaetes taurinus, Burchell)	223	7	1,561	0.1	0	0	0
Waterbuck (Kobus defassa, Ruppell)	160	20	3,200	0.2	20	3,200	0.2
Bushbuck (Tragelaphus scriptus Pallas)	50	20	1,000	0.1	20	1,000	0.1
Baboons (Papio daguera)	20	400	8,000	0.6	400	8,000	0.5
Reedbuck (Pedunca redunca, Pallas)	50	20	1,000	0.1	-	1,000	0.1
			1,421,436 **167 Kg/ha**			**1,469,686** **173 Kg/ha**	

Watson & Tarner's results when recalculated with Field & Laws (1970) unit weights where applicable, give an overall biomass of 167.2 kg/ha, even after hippo, waterbuck, reedbuck, bushbuck and baboons have been added in. Their former estimate based on Lamprey's unit weights was 218.7 kg/ha.

My Estimate of 173 kg/ha for the study period is considerably lower than the year round estimate of 295 kg/ha for typical bushed grassland habitat in Q.S.P. (Field & Laws, 1970). This difference may be related to the relative lack of hippo in Manyara, which in Q.E.P. formed 65.39 percent of the biomass in that habitat. The Manyara estimate is minimal however, and if the cryptic species were more carefully censured and if the areas below the escarpment were considered alone, the biomass estimate might be equally high.

Having confirmed that the L.M.N.P. elephant population is indeed one of the densest populations found in Africa, I now turn to the problems that naturally presented themselves: (1) How is it that the social organization of the elephants allows this high density? (2) Can the Park support this population or are there signs of over-utilisation? And, closely connected with both questions: (3) What is the reproductive status of the Lake Manyara elephant? These questions deserved study in connection with the reports on other densely populated areas (Laws et. al. 1970) which indicate over-population with resulting over-exploitation, habitat deterioration and a slow-down of recruitment.

CHAPTER 5 — SOCIAL ORGANIZATION

SOCIAL ORGANISATION

Introduction.

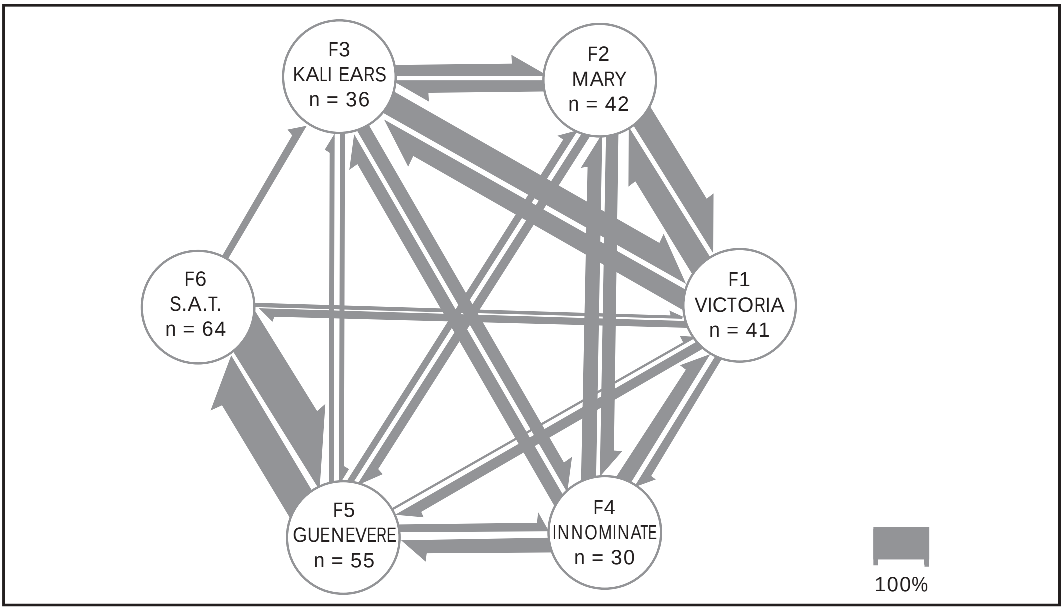
Buss (1961) was the first to suggest that a family group led by cows was the basic unit of elephant society. He described the unit as “an adult female and its offspring or two or more closely related females and their offspring”. He described them as numbering between 4 and 15, moving in a closely co-ordinated fashion often with bulls loosely or temporarily attached. As evidence for the cohesion of units he cited an observation where two groups of elephants met, intermingled and later separated out according to their original numbers.

A further analysis of the structure of elephant groups was made by Laws & Parker (1968), based on the post mortem analysis of about 700 elephants shot in Uganda and Kenya. They concluded that “the general organization was on a matriarchal pattern, an old female leading the group, which consisted of her offspring, including males up to puberty and females of all ages up to the matriarch’s age, less her age at the birth of her eldest daughter”. Other groups were interpreted as ‘extended family units’ containing sub–groups led by mature sibling daughters after their mothers had died. They also concluded that bull herds were loose aggregations of unrelated mature males with probably very slight social ties, either to any particular family or to each other.

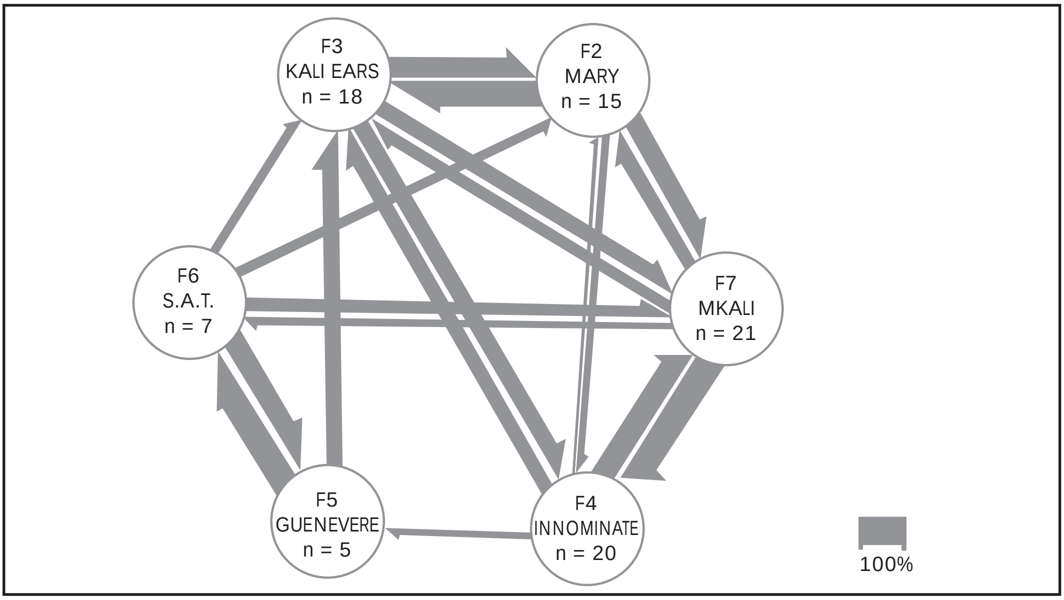
These deductions about the social organization of elephants were made mainly from relationships implied by age compatibility within groups, and cow/calf relationships suggested by the occurrence of placental scars, or by observations of lactation or suckling in the female immediately before culling. Previous to the Manyara study, long-term confirmation of the permanence of these bonds has not been made with known living animals.

The tendency of elephant families to clump into groups of 100–200 also led Laws (1969b) to suggest that “there is some indication from the aerial counts in Tsavo and in Murchison that there may be an intermediate level of organization between the family units and bull herds, and the unit population, which we may call a clan.” Initial observations at Manyara of the social structure of the elephant population, did not contradict the basic matriarchal family unit concept. The bulls were seen alone or in small groups. The cows and calves lived separately in discrete groups with individuals of all sizes seldom separated by more than fifty metres from another group member. Most of the day, they were loosely strung out, and moving in the same direction through the vegetation, giving the impression of well co-ordinated units. In moments of stress, for instance, they tended to bunch around the largest cow and follow her lead.

Figure 5.1 Nearest neighbour relationships.



A. Family unit Victoria No. 31 (1968)



B. Family unit Victoria No. 31 (1970)

Calves are excluded. The thickness of arrows indicates proportional preference of individuals for each other (See text).

The social organization of a far ranging species such as the elephant can be quantified in terms of movements and spatial relationships between individuals and groups. In this chapter the several levels of elephant society are described in these terms. Social interactions between individuals and groups and their relevance to population regulation will be discussed in the next chapter.

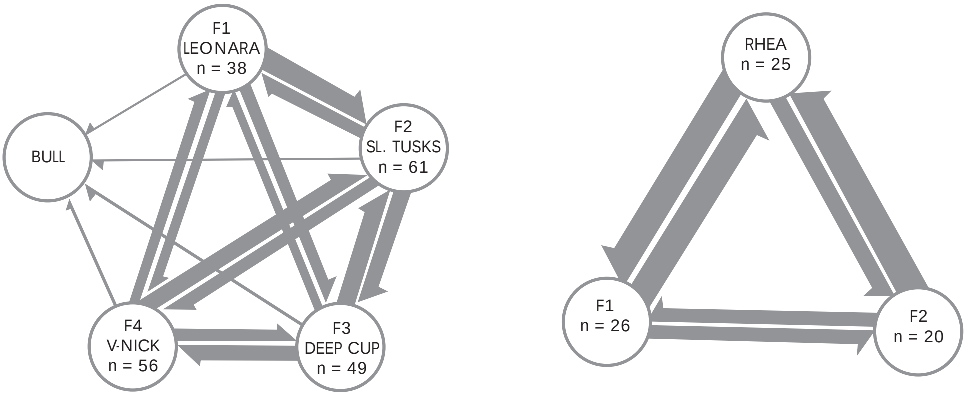
Nearest Neighbour Relationships

A practical difficulty in making observations in Manyara was the poor visibility, which meant that usually only one or two elephants of a group could be seen at a time, and then probably for only a few minutes. It was unusual to be able to observe an elephant for as long as ten minutes without interruption even in the relatively open Acacia tortilis woodlands. One possible method under these conditions was the recording of nearest neighbour relationships, as it was often possible to record the nearest neighbours of whichever individuals were visible at one time. The proportion of times that an individual stood nearest to another out of the number of times that it was observed standing nearest to any elephant, was taken as an indication of its individual preference for that other animal. For instance, each calf would almost always stand nearest to a particular female, presumably its mother. The preferences of individuals of other ages too were so strong that it was relatively easy to define discrete cow/calf groups, without needing to use any statistical sorting processes.

As each group became clear, I gave the individuals names. When referring to a group I used the first three letters of the matriarch's name in capitals, followed by the letters F. U. , which stand for family unit; a concept which my observations support.

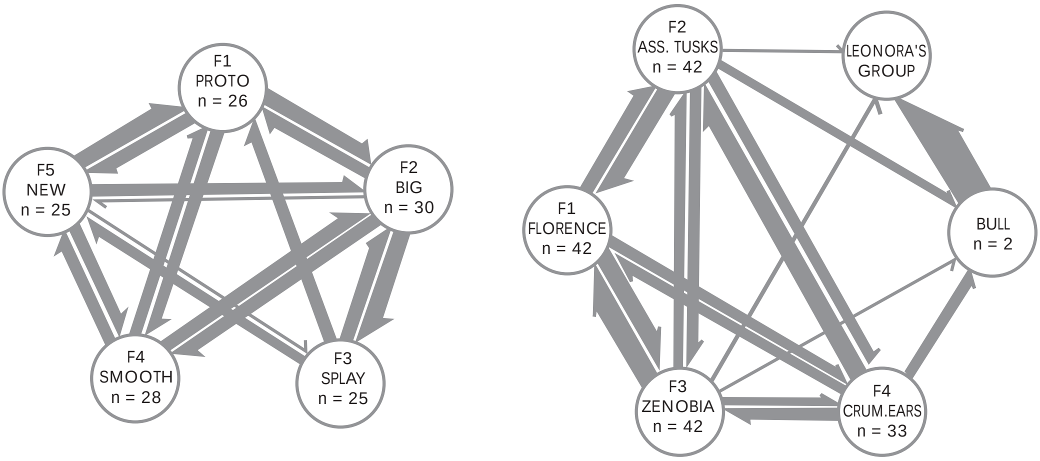
Detailed observations made on five different family units demonstrate the consistency of nearest neighbour choice. Figure 5.lA is a sociogram illustrating typical relationships of six adult cows of a group named VIC F.U. Calves are excluded from this diagram in order to isolate the adult relationships. The thickness of each arrow passing from one cow to another is proportional to the percentage of times that she stood nearest to the other (N = 268). The records were collected between June and August 1968 (Appendix, 3.1). Each observation was separated from the next by at least five minutes, during which time most of the elephants would have moved, thus increasing the independence of successive observations. Figure 5.lB represents the nearest neighbour relationships of the same family over a four-day period in August 1970 (N = 102, Appendix 3.2). The long–term integrity of the group is demonstrated by the fact that in these two sets of observations no member was seen as the nearest neighbour of any of the other 420 elephants with overlapping ranges. The only changes amongst the adult females that occurred were caused by the death of the leading matriarch, Victoria, and the maturing of a young female, Mkali, who became pregnant at the age of approximately 10 years, and who has been treated as an adult female in the 1970 set of observations.

Figure 5.1
Nearest neighbour relationships



A. Family Unit Leo (1970)

B. Family Unit RHE (1970)



C. Family Unit OLD (1970)

D. Family Unit FLO (1970)

Calves are excluded. The thickness of arrows indicates proportional preference of individuals for each other (See text).

Figure 5.3

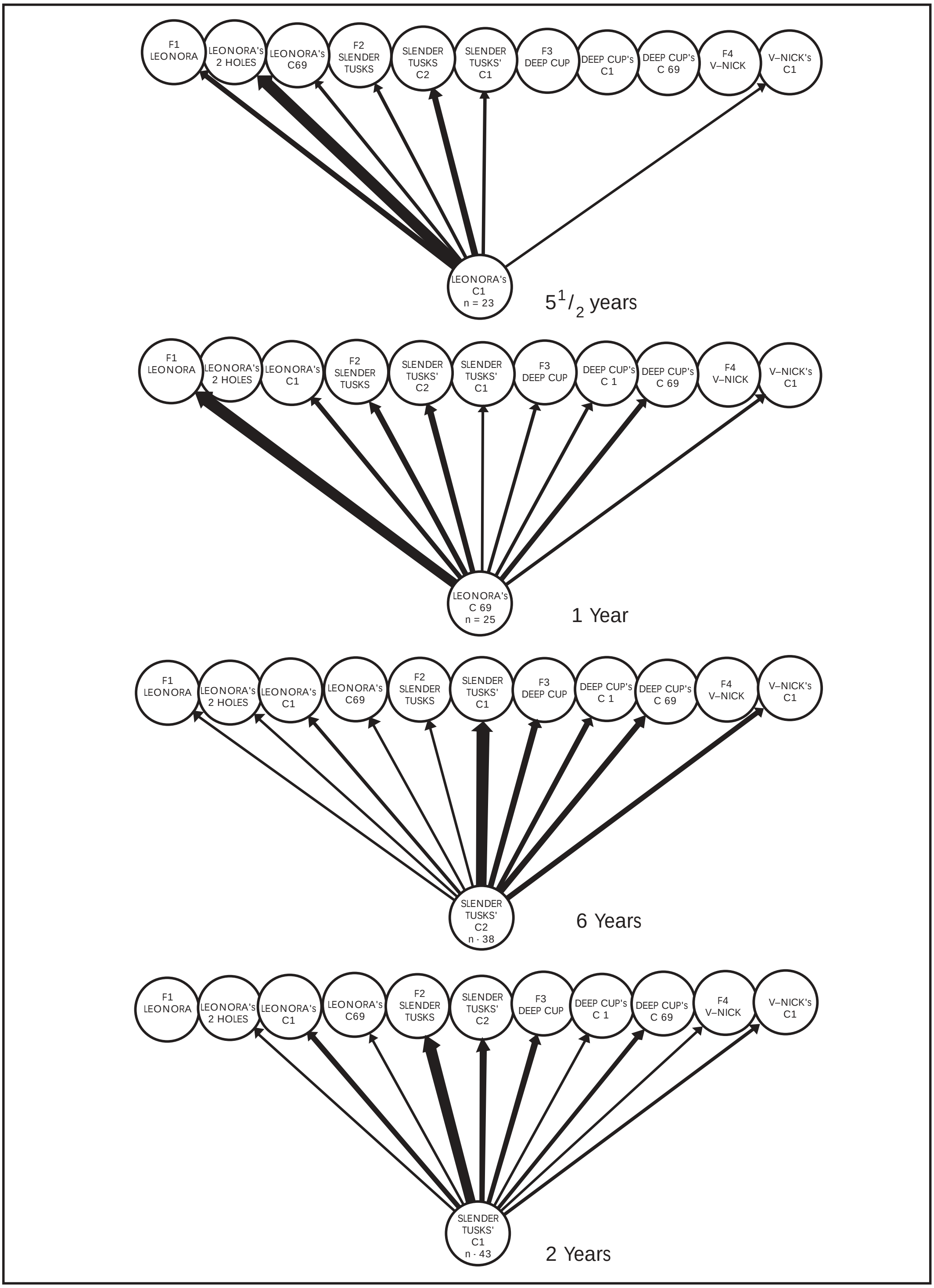
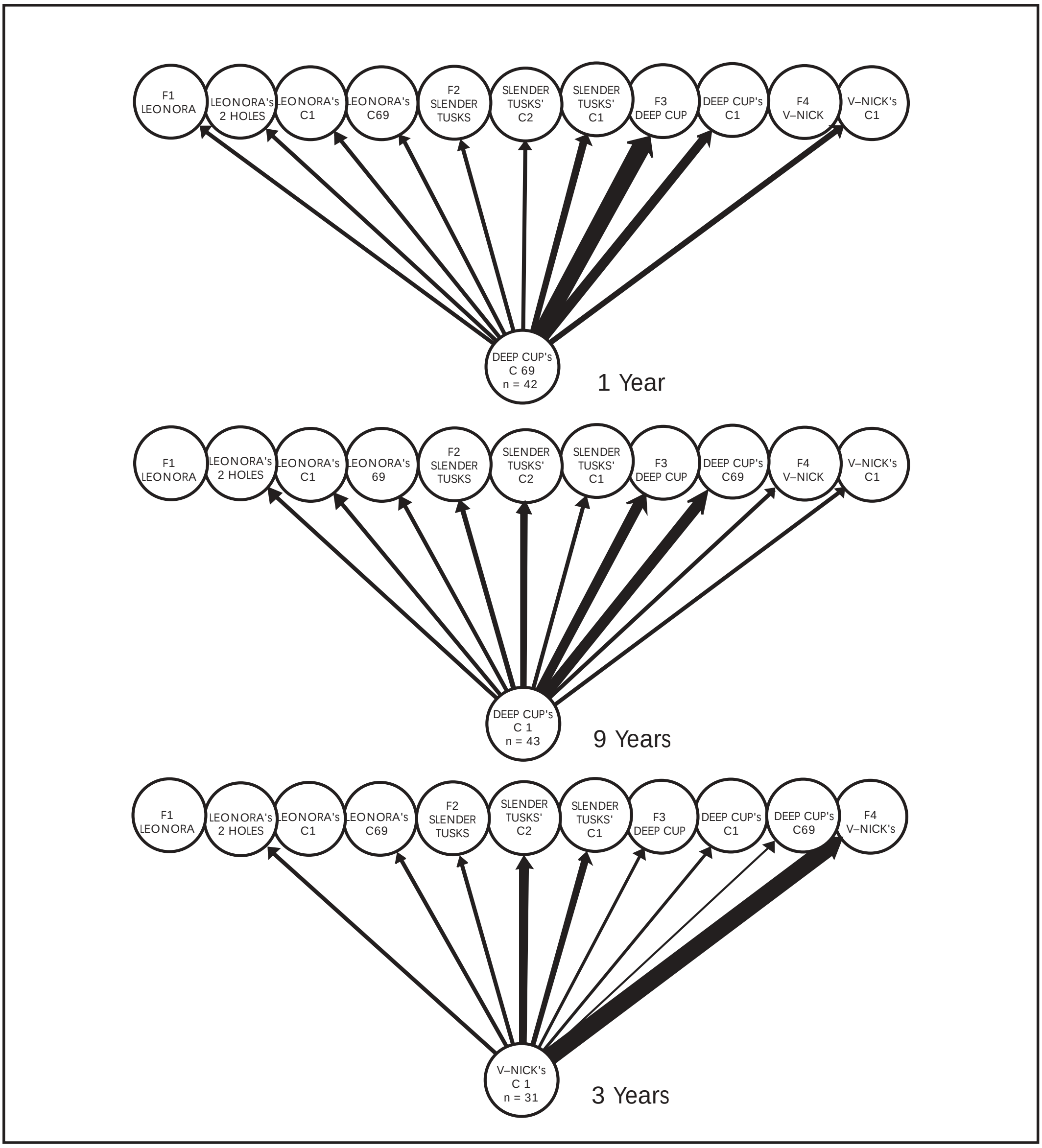

F1 LEONORA
LEONORA's 2 HOLES
LEONORA's C69
F2 SLENDER TUSKS
SLENDER TUSKS C2
SLENDER TUSKS' C1
F3 DEEP CUP
DEEP CUP's C1
DEEP CUP's C 69
F4 V–NICK
V–NICK's C1
LEONORA's C1 n = 23
$5^1/_2$ years
F1 LEONORA
LEONORA's 2 HOLES
LEONORA's C1
F2 SLENDER TUSKS
SLENDER TUSKS' C2
SLENDER TUSKS' C1
F3 DEEP CUP
DEEP CUP's C 1
DEEP CUP's C 69
F4 V–NICK
V–NICK's C1
LEONORA's C 69 n = 25
1 Year
F1 LEONORA
LEONORA's 2 HOLES
LEONORA's C1
LEONORA's C69
F2 SLENDER TUSKS
SLENDER TUSKS' C1
F3 DEEP CUP
DEEP CUP's C 1
DEEP CUP's C 69
F4 V–NICK
V–NICK's C1
SLENDER TUSKS' C2 n · 38
6 Years
F1 LEONORA
LEONORA's 2 HOLES
LEONORA's C1
LEONORA's C69
F2 SLENDER TUSKS
SLENDER TUSKS' C2
F3 DEEP CUP
DEEP CUP's C 1
DEEP CUP's C 69
F4 V–NICK
V–NICK's C1
SLENDER TUSKS' C1 n · 43
2 Years

Figure 5.3



Nearest neigbour choice of calves in LEO family unit. The thickness of each arrow is proportional to the preference of a calf for a certain individual. Calves tended to stand nearest to either their mothers or to their siblings.

Occasionally a bull or a member of another group might appear in these nearest neighbour records as in Figure 5.2 A&D which summarizes the individual preferences of the adult cows of four more family units over a period from July to September 1970. (Appendix, Tables 3.3–3.8). Such bull attachments were weak and short–lived, lasting perhaps up to ten days at the most, often during the oestrus period of one of the cows.

In these groups, cited as typical examples, the calves have been left out in order to simplify the picture. Their nearest neighbour preferences show their strong attachments to particular adult females. A typical example is V–Nick's calf which stood nearest to one adult female, V–Nick, 18 times out of 31, when it had a choice of eleven other elephants in LEO F.U. (See Figure 5.3 and Appendix 3.7).

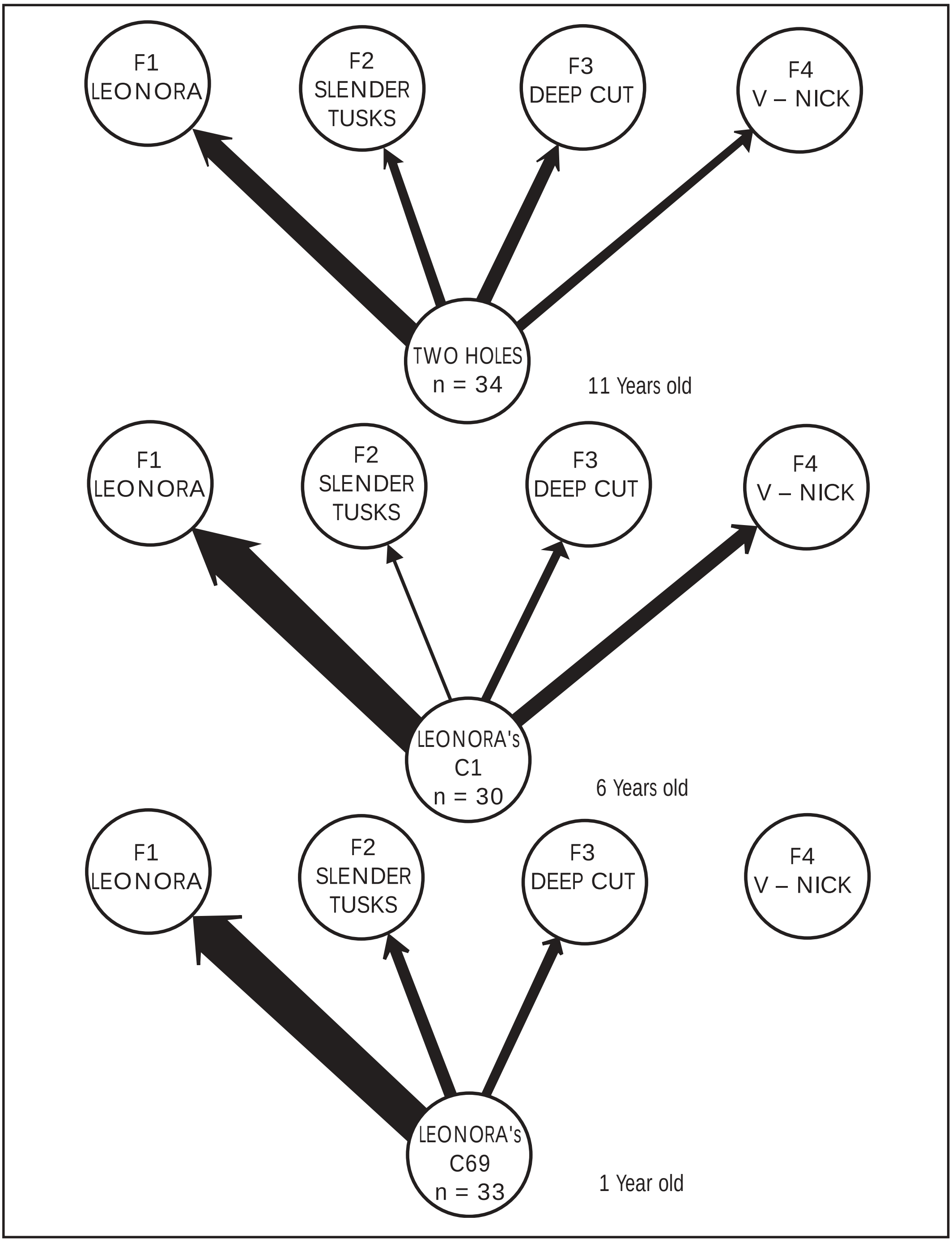
It is plain that each calf showed a strong preference for a particular female. I have referred in each case to the preferred female as the mother, although occasionally I may be mistaken since case histories of orphaned calves show that an orphan may have a preferred female after its mother has died. In the next chapter this assumption is further justified by the observation that three known calves from birth consistently exercised their nearest neighbour choice in favour of their mother. The older the female is, the more likely she is to have several calves attached to her. Consequently siblings, which are attracted to their mother, tend to have high scores relative to each other.

Nearest neighbour scores also suggest that the younger a calf is, the higher will be the proportion of "nearest to mother" observations. Figure 5.4 illustrates this point by showing the strength of association of Leonora's three calves of 11, 6 and 1 years old, in relation to all the adult females of LEO F.U. It seems that the youngest calf of one year old is stronger in her attachment to Leonora than the six year old (Appendix, 3.8). This tendency is confirmed in the next chapter.

Nearest neighbour records also show that a female calf's bond with its mother may remain strong even after it has become mature, as in the case of Mkali with her mother, Innominate, of VIC F.U. Figure 5.5 (Appendix 3.7) illustrates Mkali's nearest neighbour preference, during the two periods separated by two years already described for this group. It will be noted that in both periods Mkali tended to stand nearest to her mother rather than any other female. This mother/female calf relationship is highly variable, however, and although there is evidence that the bond may last almost a lifetime, this does not always appear to be the case.

In some groups each adult cow seemed equally attracted to all other cows, but in others strong sub–groups were seen, in which two or more adult females tended to stand together and move slightly apart from the rest of the group. VIC F.U. contained one such sub–group consisting of S.A.T. (Short Asymmetrical Tusks) and Guenevere, two young females with one and two calves respectively in mid–1968. This sub–group remained consistent over

Figure 5.4



Leonora's nearest neigbour choice of three calves. The proportion of observations of calf nearest to mother decreases with the age of the calf.

the following two years and the attraction of these two animals for each other is reflected in the thickness of the arrows linking them (Figures 5.lA and B), and in the relative weakness of their ties with the others. The development of such sub–groups and the eventual splitting of family units is described below.

Structure, Number and Size of Family Units

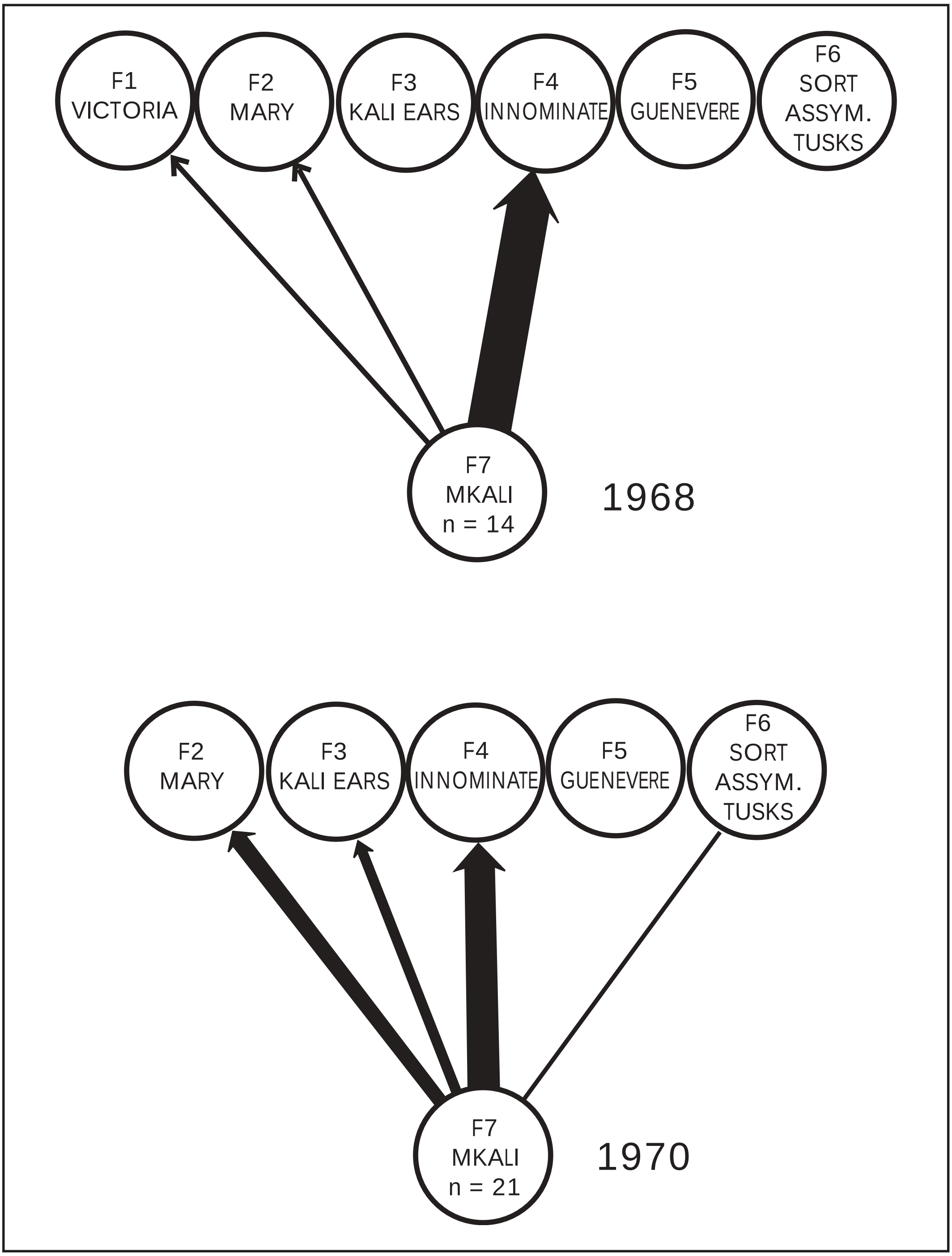
On the basis of over 15,000 independent observations of known individuals over a period of 4 1/2 years I was able to distinguish 48 separate cow/calf groups, within the Manyara study area. (Sightings per unit appear in Fig. 4.4. A sample of 25 groups were selected for special study, and by the middle of 1967, I was able to recognize every individual. I followed the development of these groups until mid–1970. By assuming cow/calf relationships from nearest neighbour observations, and by ageing the animals from their shoulder height (see Chapter 3,), it was possible to construct diagrams summarizing the age structure and some of the relationships within each family unit. Continuing with VIC F.U. as an example, Figure 5.6 shows the age structure of this group. Each calf is placed beneath the female to which it stood nearest most frequently and that female is assumed to be the mother. Adult females are only accorded approximate size categories as the method of ageing, based on the shoulder height, precludes reliable estimation beyond the age of fifteen years. The adult females are also almost certainly related to each other in most cases, but their exact relationships cannot be deduced from nearest neighbour preferences as the bond between female siblings, as they grow up, in some cases appear to become stronger than the bond between a mother and her daughter.

However some of these groups could be interpreted in Laws & Parker's categories, as "matriarchal" with mother and her mature female offspring and their calves, or as "sibling" groups, of mature sisters with their offspring, or as a combination of the two. Any group larger than one mother and her immature offspring should be called an "extended family unit", but as the units were clearly integrated, cohesive, and stable, I will refer to them in one category, based on spatial criteria, as "family units", which is also consistent with previous nomenclature. (Buss, 1961; Laws & Parker, 1968; Laws in press, 1972).

The age structure in mid–1970 of each of the sample F.U.s is summarized in Appendix 4 and will be further discussed in Chapter 8 on Population Dynamics.

The family units varied in size from 2 to 24 animals with means and medians that fell between 9 and 11, for all the years. Figure 5.7 shows the distribution of the family unit sizes of this sample over four years. In comparison the mean size of 59 mixed herds in the M.F.P.S. sample, referred to by Laws (in press 1972) as family units was 11.6. This mean would be marginally lower if the temporarily associated bulls were subtracted from the total, and probably would not differ significantly from the mean family unit size of Manyara, which in 1970 was 10.8 (± S.E.

Figure 5.5



Nearest neigbour preferences of Mkali, a female aged ten in 1968, for adult females before and after her first pregnancy. Her calf was born in 1971.

Figure 5.6
VIC family unit. Age structure and mother offspring units.

(Sex given when known)

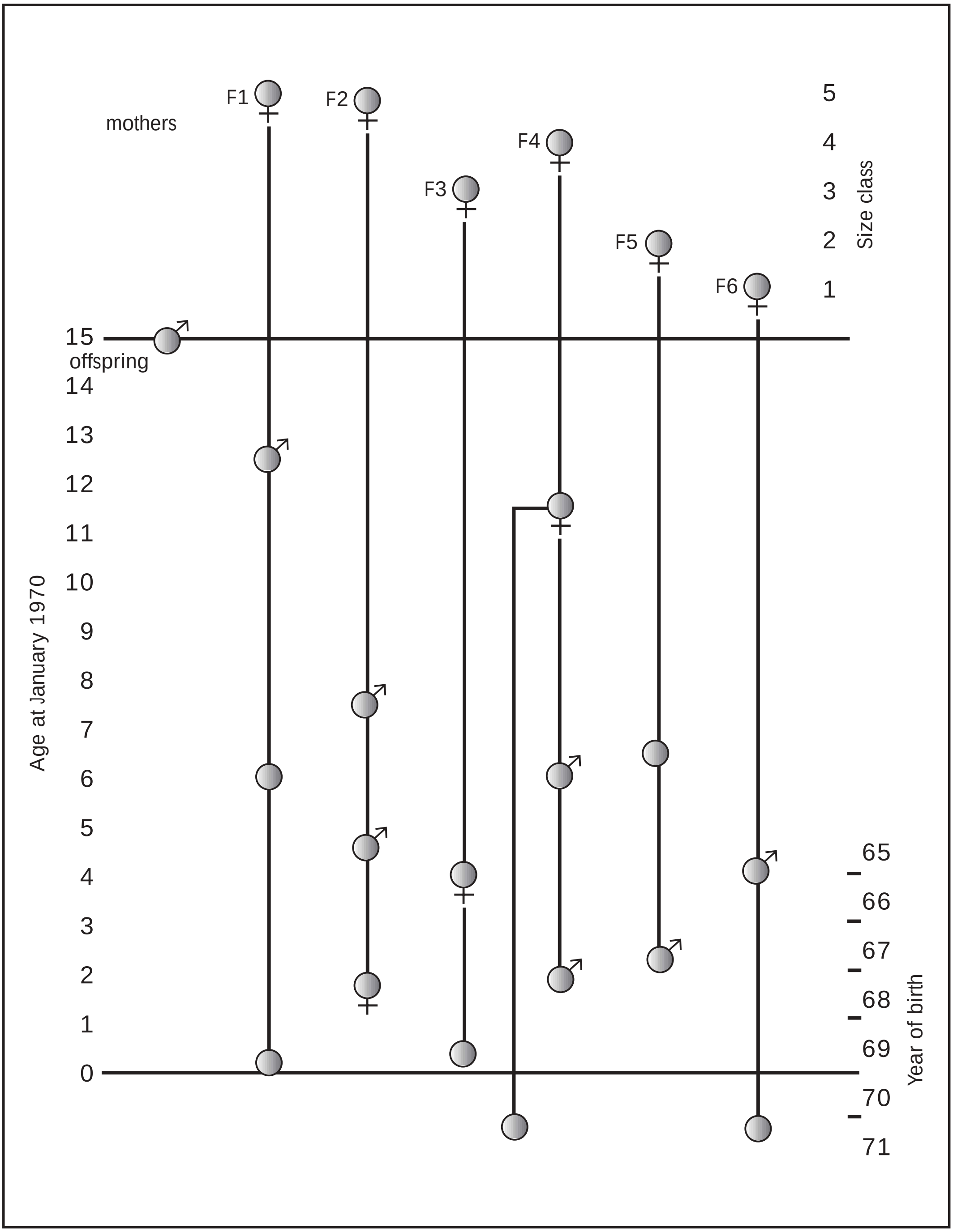
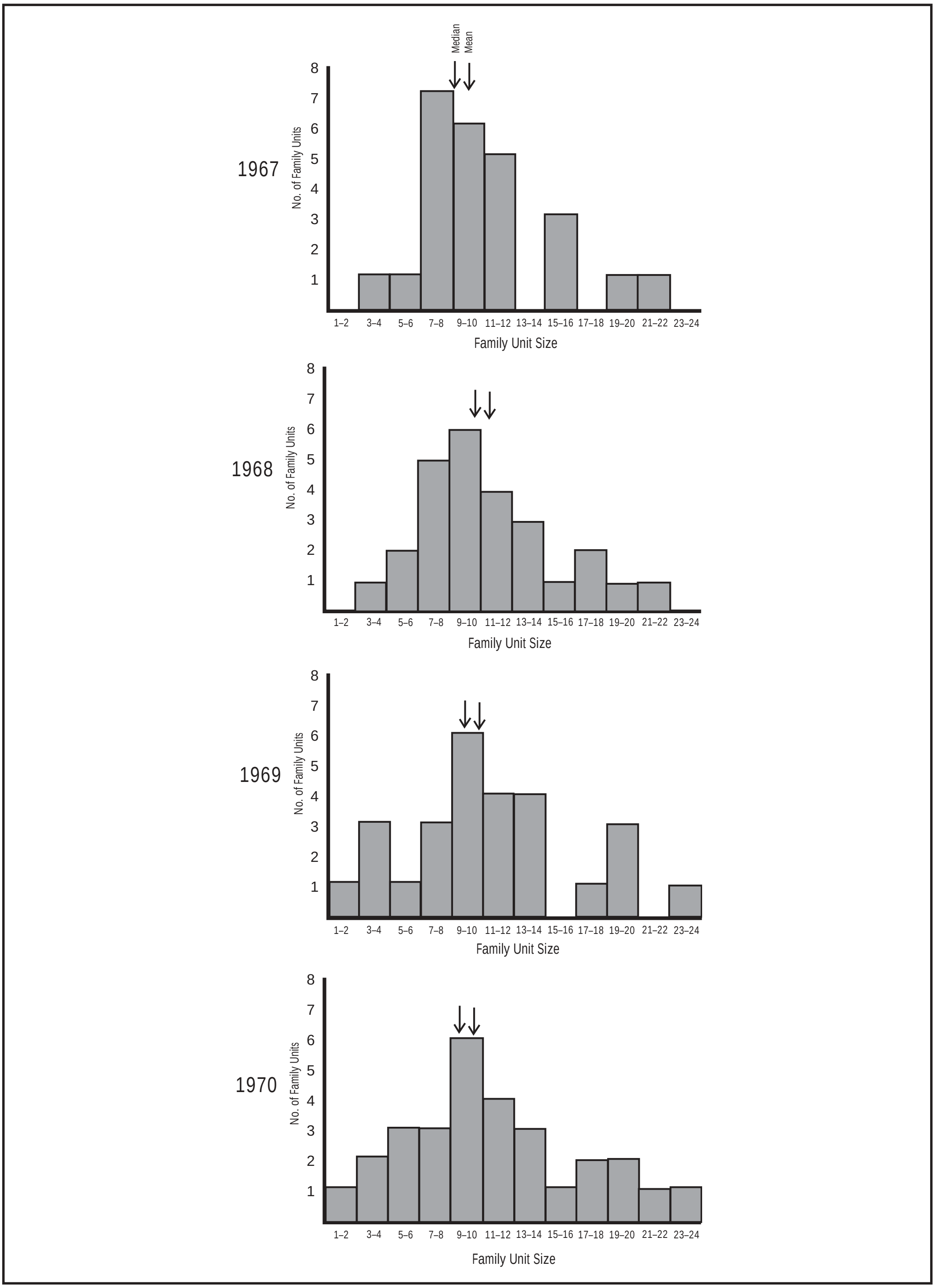


Figure 5.7
Frequency distribution of family unit size



0.96). In Manyara there were on average 3.6 mother–offspring groups per family unit, compared to 2–3 per family unit in M.F.P.S. (Laws in press). The mean size of mother–offspring groups was 3 at Manyara compared with 2.75 at M.F.P.S. which is related to a difference in recruitment (Chapter 8). The slight changes from year to year in the size frequency distribution of Manyara family units were caused by births, deaths and the few animals which left their own unit and are summarized in Appendix 5. Apart from these changes, each group contained exactly the same cows, each with its followership of calves in mid-1970, as it had in mid-1967. I conclude that the family units, determined by this spatial analysis, correspond closely to their Murchison and Tsavo counterparts, and confirm that they are the basic stable units of elephant society.

Exceptions to Family Unit stability

The years of the study period were years of increase for the elephant population (Chapter 8), and three of the units which had increased in size split to form new groups, which were themselves stable. Splitting was a slow process, developing over years. At first distinctive sub-groups would appear, and gradually they would spend more time further apart. I arbitrarily judged a split to have occurred when two sub–groups had separated by a distance of one kilometre which could reasonably be assumed to exceed an elephant's range of vocal communication, by which they normally keep contact.

For example, BOA family unit in mid-1967 had 22 animals. It was then the largest family unit in the Park. By mid-1968 two distinct sub-groups could be distinguished. One sub-group contained two young cows, Isabelle with two young calves, and Laila, who probably was Isabelle's daughter. They gradually became more independent of the main group, which contained the older cows and their calves. From being within 50 metres of the main group the average distance of the sub-group slowly increased. This independence accelerated when the younger cow, Laila, gave birth to her first calf. They tended now to linger at ever increasing distances from the main group, and it was often difficult to tell whether they were still in contact with them or not. One day when they were a little removed in this way, the matriarch of the main group, Boadicea, led her family over 15 Km to the South and the sub-group remained behind. This was the first time I had ever seen them separated by more than 1 km., although I had been in constant touch (No. obs. of BOA F.U. = 314). If 1 Km is used as a criterion, the group had split. When the main group returned from the South the sub-group once more associated with them much more than with any other family, remaining within a looser but nonetheless real association.

I also recorded the complete process of splitting in Family Units HEL and POR. Five other groups showed splitting tendencies but were not seen to exceed the 1 Km limit.

Table 5.1: Relative sizes of cows in family units with sub–groups

Adult Cows in Sub Groups

		FU 01 AET–(CYG)		FU 06 ARI–(BOT)		FU 07 BOA–ISA		FU 12 HEL–F3	
	5					1			
Size Class	4	1		1		2		1	
	3	1			1	1	1		
	2		2		2	2		1	1
	1	1	1	1			1		
TOTAL COWS		3	3	2	3	6	2	2	1
SUB–GROUP TOTAL		9	8	9	13	18	5	7	2

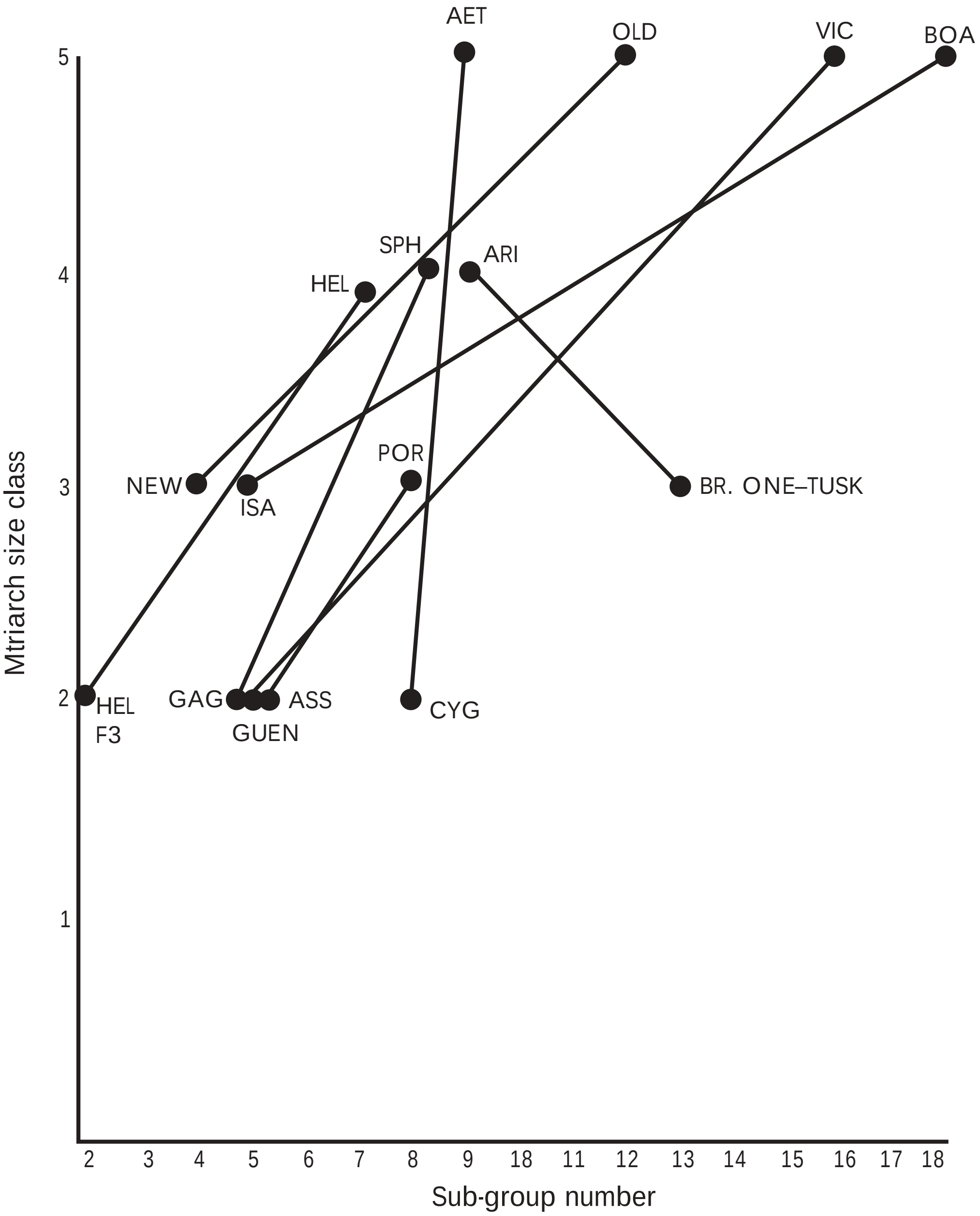
		FU 21 OLD–NEW		FU 26 POR–ASS		FU 27 SPH–(GAG)		FU 31 VIC–(GUE)	
	5	1						2	
Size Class	4	1				1		1	
	3	1	1	1	1	1	1	1	
	2	1		1	1		1		1
	1				1		1		1
TOTAL COWS		4	1	2	3	2	3	4	2
SUB–GROUP TOTAL		12	4	8	5	8	5	16	5

The relative sizes of the mature cows, in these family units and the number in each sub-group appear in Table 5.1 opposite. It appeared to me that there was a tendency for sub-groups with small, therefore young, matriarchs to split from sub-groups led by large, therefore old matriarchs, but the sample was too small to demonstrate this statistically. However in seven cases out of eight the largest sub-group also had the largest matriarch (see Figure 5.8 overleaf). Apart from one exception below, there was no tendency for the younger matriarchs to change their range; on the contrary they tended to follow the parent group.

“Splitting” embodied no sharp point of separation and the progression of the sub-group to independent family unit level was part of a continuum.

All of the animals which left their family units on their own were young males which had reached the age of puberty. At this stage of development, young males

Figure 5.8
Size of matriarch relative to group size.



In this diagram, the sub-group matriarchs of each family unit which split or showed splitting tendencies, are joined by a straight line. It is demonstrated that the larger matriarchs tended to lead the larger sub-group.

are customarily expelled from their family units by active rejection on the part of the mature females, and after following the family at a distance, they eventually become completely independent, retaining no significant association with their former families.

Only in one isolated instance did a young female leave a family (HEL F.U.) with her calf, change her range, and possibly join up with young females belonging to another family unit (GAP F.U.), but these associations were based on less than 15 observations of this individual. Apart from this example no individual was seen to leave one group and join permanently with another. The fact that I only saw this in one group out of 48 suggests that the great majority of the units are composed of closely related animals. In short, groups grew by reproduction, split up when numbers increased, but were seldom if ever formed by integration. Thus the term ‘family unit” is further justified.

Occasionally individuals were seen separated by more than 1 kilometre from their family unit, but these separations only lasted for periods of a few hours to one day at the most, and it is probable that the individuals concerned had only temporarily strayed. One sub-adult female of 12 years (Phoebe, of ANI F.U.) was seen on eight consecutive occasions more than five kilometres from her unit. For about a fortnight she tried to associate with strange family units, but was rejected; later, however, she rejoined her unit and I infer that she had accidentally lost touch.

Bull Groups

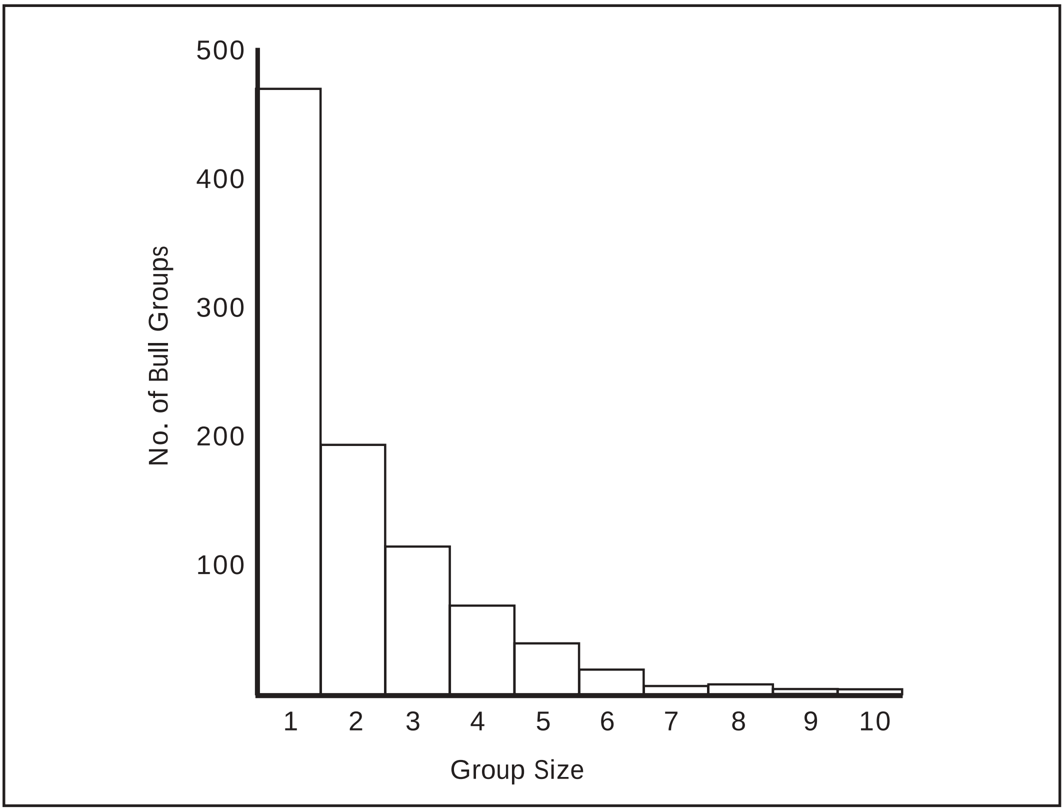
A bull elephant in its daily movements seeks the company of other elephants, and tends to join other groups of cows and bulls, following them or moving in parallel. Bulls were seldom seen in circumstances where they might have been out of communication range with other elephants. Out of a sample of 969 observations of individual bulls within the study area between 1966 and 1968, the probability that an individual bull would be seen within 1 Km. of another bull without cows was 50 percent, within 1 Km. of a cow/calf group without bulls 11 percent, and within 1 Km. of adults of both sexes 21 percent. In only 18 percent of the observations were bulls seen apparently more than 1 Km. from the nearest elephant, and this percentage is undoubtedly high as I was often unable to detect the whereabouts of the nearest elephant due to low visibility. There were no significant seasonal change in wet and dry month probabilities pooled over the three years. ($X^2 = 1.06$, $p > .l$) (Appendix 6.1).

In examining exclusively bull associations I defined a bull group as an association of bulls in which no member was more than 200 metres from the next. However, two bulls that were obviously passing in different directions would not be grouped together, whereas two bulls which had been following each other for several hours would be included even if they had exceeded the arbitrary 200 metre distance. Bull groups were classified independently of the presence or absence of cow/calf groups.

Bull groups varied in size from 1 to 10. The frequency distribution of bull group size is illustrated in Figure 5.9. No significant variation between wet and dry seasons was shown by a Kolmogarov Smirnov test ($X^2 = .42$, $p > .1$, Appendix 6.2). This distribution with a mean of 2.1 is similar to that described by Laws (1969b) for bull groups in Tsavo, with a mean of 2.43; although his method of aerial estimation was quite different. Subjective differences in defining a group may partially account for differences in the size of bull herds reported from other areas, but bull herds have been reported as large as 33 and 47 in the Serengeti (Dr. H. Lamprey, pers. comm.), 50 in the Imatong mountains South Sudan (Anderson, 1950), 35 in Tsavo (Laws, 1969b), and 144 in the Galana area, Kenya (Parker, pers. comm. in Laws, 1969b).

In some ranges bull areas exist where few or no cows are found, such as Seronera in the Serengeti (Hendrichs, 1971), Ngorongoro Crater floor (Mr. O. Saibull, pers. comm.), parts of the Kruger National Park (Pienaar et. al. 1966), the Imatong mountains of South Sudan (Anderson, 1950) and parts of the Tsavo (Laws, 1969b). It appears that where elephant populations invade new areas the bulls are the first to arrive (Pienaar, 1963; Lamprey et. al. 1967).

Figure 5.9: Frequency distribution of male group size, 1966–1969.



Bull groups were very unstable at Manyara, and their numbers fluctuated from day to day. The longest I ever saw two bulls remain associated was for fourteen consecutive days. One bull M.9. with a shoulder height of 264 cms. and an estimated age of 20 to 25 years, was immobilized and radio tracked for 22 days. During that time he associated with 12 different bulls, both larger and smaller than himself, and with four different family units. None of the associations with individual bulls lasted unbroken for longer than five days, nor with family units for longer than one day.

Over three years I kept a record of bull associations and the results are summarized, for the 25 most commonly seen, in Table 5.2. The highest score occurred between males 14 and 10, which were seen together 61 times. However, both these animals were also seen more often in total, partly because they were exceptionally tame, and partly because they were easy to recognize.

Table 5.2: Associations and sightings for years 1966, 1967 and 1968 of 25 most commonly observed males.

Male code number																										
6	7	8	9	10	11	12	13	14	15	16	17	19	21	22	24	27	35	36	39	40	54	56	63	Total Associations	Times seen	Male code number
2	0	0	1	3	3	2	1	6	0	0	1	0	2	0	1	0	0	1	0	1	1	0	1	25	37	1
	0	1	7	23	3	15	2	10	0	10	0	3	2	1	1	0	4	3	1	1	7	9	0	105	72	6
		1	11	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	5	27	7
			1	0	0	2	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	7	13	8
				16	3	10	1	11	2	2	0	2	6	1	0	0	5	2	0	3	3	7	0	84	106	9
					10	42	3	61	5	12	1	10	15	0	0	0	3	4	1	1	14	25	0	249	180	10
						6	0	8	0	0	1	1	1	1	0	0	0	1	0	0	4	3	0	45	40	11
							4	30	5	8	1	8	8	1		0	2	3	0	1	3	8	8	159	132	12
								5	0	0	0	1	3	1	0	0	0	2	0	1	0	0	0	24	18	13
									6	3	2	8	12	0	1	1	6	6	3	1	12	20	0	213	158	14
										2	1	0	0	0	0	0	3	2	1	0	0	2	0	30	45	15
											0	4	0	0	0	0	4	0	1	0	4	9	0	59	48	16
												2	1	0	0	0	1	0	0	0	0	0	0	11	17	17
													1	1	0	0	3	0	0	2	1	1	0	48	64	19
														0	0	0	1	3	0	0	0	1	0	56	51	21
															0	0	0	0	0	1	0	0	0	7	12	22
																0	0	0	0	0	0	0	0	3	5	24
																	0	0	0	0	0	0	0	1	13	27
																		0	2	0	1	6	0	43	68	35
																			1	0	2	1	0	31	27	36
																				0	0	3	0	13	16	39
																					0	0	0	12	20	40
																						9	0	61	39	54
																							0	104	41	56
																								1	14	63

In order to test whether any of these associations were statistically significant, and hence might be caused by individual ties, it was necessary to calculate the expected number of associations for each pair on the null hypothesis that all males associated at random. The expected value for each pair may be calculated from the total associations of each partner and the grand total of all males, according to the following formula, which was suggested to me by Dr. M. Cullen:

$$E_{AB} = \frac{a\ b}{2}\left(\frac{1}{N-a} + \frac{1}{N-b}\right)$$

Where: E_{AB} = Expected number of associations for cell AB

a = Total associations of elephant A
b = Total associations of elephant B
N = Grand total of all associations in matrix.

This formula calculates the expected value irrespective of differences in the probability of sighting individuals. The statistic;

$$X = \frac{\overline{0 - \sum}}{\sqrt{E}}$$

where 0 = Observed value and E = Expected value, gives a rough estimate of the standard error of the difference of the observed from the expected. Thus the strength of association can be measured as the number of standard errors that the observation is away from its expected value. (Andrew, 1956). Only the 0.01 level of significance (Z = 2.58) was used because of the approximate nature of this test. An example will clarify the procedure. The two bulls, 14 and 10, had the following association values:

Observed Associations = 61

Expected Associations = 45.54

$$\frac{O - E}{\sqrt{E}} = 2.29$$

$$P > .01$$

Consequently the association was not shown to be greater than the level of chance.

The same calculation was performed by computer for each cell in the association matrix, but over the three years none of the bulls could be demonstrated to be significantly associated with any other, despite the fact that some of the expected values were less than five, which using this method would tend to produce some cases of spurious significance.

Similar association data for bulls have been collected by Hendrichs (1971) and Croze (pers. comm.), in the Serengeti. Using the same method, I tested their association matrices, this time excluding pairs with expected values less than five. There were 25 bulls in both matrices and some of Croze's bulls were the same as those of Hendrichs. Only one pair showed any significant association, Hendrichs' bulls 18 and 30. (0 = 15, E = 6.96, Z = 3.05, p < .00l). This one exception may perhaps be explained by intensive short–term sampling, or small sample size.

These observations provide the first long-term evidence to support the hypothesis of Laws & Parker (1968), that bulls have very slight social ties, either to each other, or to any particular family unit within their home range. If there are any exceptions to this rule they are probably rare, but in an animal as complex and intelligent as an elephant with such wide variations in individual behaviour a small proportion of unusual bonds between bulls would not be surprising.

Family Unit Spacing and Movements

In looking at levels of organisation above the family unit, it is necessary to examine inter–group spacing and group movements on as large a scale as possible, and then to analyse how these are related to other groups within the immediate range of social contact, and to other possible environmental influences.

Family units tend to aggregate and move around in what might be described as feeding assemblages. The tendency to aggregate results in the entire population occupying only 7 percent of the available area, on average, at any one time. From the air elephants can usually be defined as clusters of discrete groups, each group being composed of one or more family unit possibly with bulls attached. The overall size frequency distribution of 591 groups seen from the air from 1966 to 1970 is illustrated in Figure 5.10. The mean group size was 9.8, but many groups which appeared homogeneous from the air were well in excess of 24 animals, which was the largest family unit size as defined by registration. Therefore some family units were intermingled with others. The

Figure 5.10: The size frequency of elephant groups from aerial census and reconnaissance flights 1966–1970.

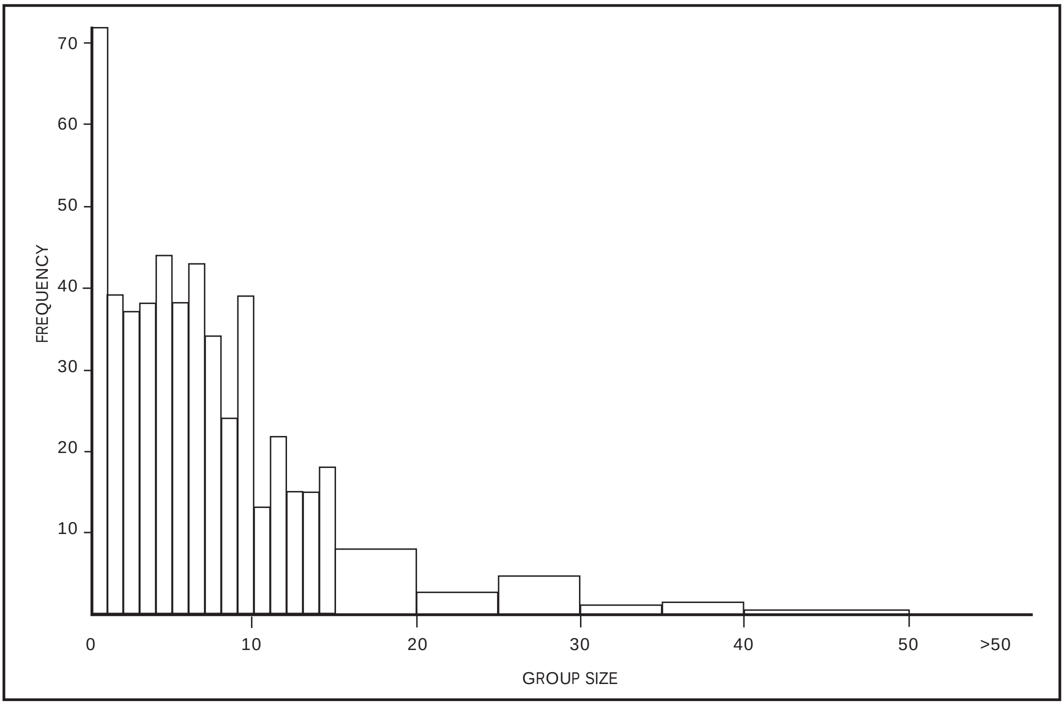
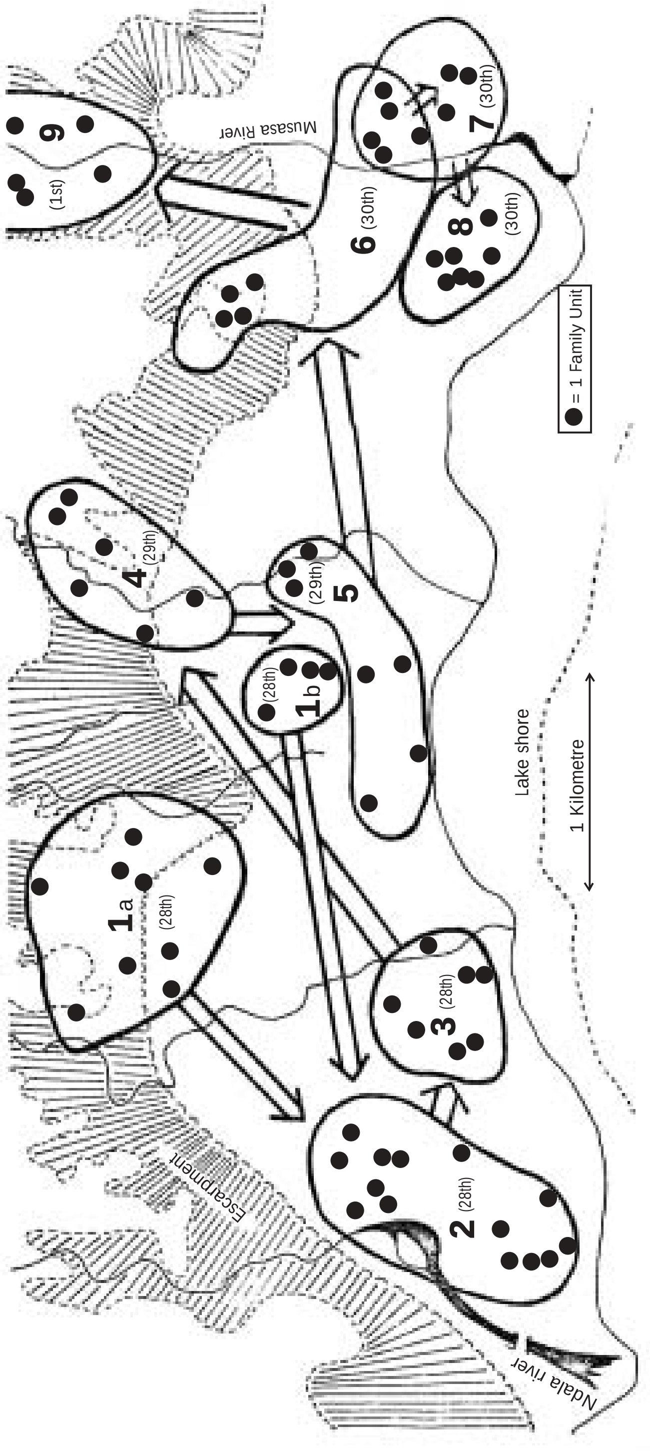


Figure 5.11: Feeding assemblage movements 28 November–1st December 1968.



Successive clusters of family units, found together for a given period (see text table 5) are delineated and numbered sequentially 1–9.

distances from the centre of each group to the centre of the nearest neighbouring group were measured from the flight maps, and showed a medium inter–group distance of 500–700 metres. Neither group size nor inter–group spacing plotted from the air could be shown to vary seasonally to any significant degree (p > .05, Appendix 6.1 – 6.6), but this inference is qualified in the next chapter.

On the ground by moving from group to group, just staying long enough with each to recognize its identity, I found it possible to plot the overall movements of some of the assemblages from hour to hour, despite the thickness of the vegetation. For example, Figure 5.11 illustrates the movements of one feeding assemblage over four days. The aggregations of family units at different periods of the day have been indicated by encircling their positions. This feeding assemblage was co-ordinated over the four days, and during that time covered most of the area on the map in a cyclical manner. The cohesion was only temporary; every day some units would join and others would leave, while some were probably present which I failed to locate. Table 5.3 below summarizes the family units and bulls identified in each of the aggregations formed during the four days.

Table 5.3: Constituent family units or bulls found in each assemblage marked sequentially on the map. (Figure 5.12)

28th November				29th November		30th November			1st December
8.00 - 10.30	11.15 - 11.20	11.45 - 14.40	16.30 - 17.00	8.40 - 10.30	13.45 - 18.10	8.20 - 10.10	14.00 - 16.00	16.55 - 17.20	8.00 - 10.00
Sequence 1a	1b	2	3	4	5	6	7	8	9
ANI					ARI	ARI	ARI	ARI	
	AET	AET	AET						
	HEC	HEC							
BOA		BOA	BOA	BOA	BOA	BOA			BOA
JEZ		JEZ	JEZ	JEZ	JEZ	JEZ			JEZ
LEO						LEO			LEO
CAT		CAT	CAT	CAT		CAT		CAT	
JAG		JAG				JAG			
		HEL	HEL	HEL		HEL		HEL	
	JOC	JOC							
		SAR		SAR	SAR			SAR	
RHE		RHE	RHE			RHE	RHE		
		POR		POR	POR	POR	POR	POR	
		OLD					OLD	OLD	
VIC			VIC						VIC
	FLO	FLO							FLO
	AGD		AGD			AGD	AGD	AGD	AGD

On the fifth day the assemblage dispersed and a new one formed, composed mainly of other groups in a different part of the Park. Such large associations usually lasted no more than a few days although they appeared very striking in the short term. The mean number of family units encountered on the ground within a radius of 1 km. of each other was 2.5, (N = 4197), but low visibility undoubtedly made this an underestimate; the maximum observed was 16 family units within a radius of half-a-kilometre. The mean numbers of family units associated were slightly higher in the wet months than in the dry months, hut when tested by Student's 't' test the differences were not show to be significant (df. 36, $p > .05$; Appendix 6.6; further discussion Ch. 6).

Rates and Patterns of Movement

Two family units, BOA and JEY 1, and one bull, M.9, were radio tracked in Manyara, together with one family unit in the Tarangire National Park, for periods of 22 days to four months. Another family unit in the Serengeti was radio tracked, with Dr. Harvey Croze, for four days. Their movements were compared by measurements of the straight line distances between radio fixes made at specific time intervals (Maps, Figure 5.18) in the section below on Home Range). The results and a discussion of differences in rates of movement have been published (Douglas-Hamilton, 1971) and appear in Appendix 7.

In Manyara fixes were usually made at dawn and dusk. The straight line daily movements varied between 0.2 and 8.2 km., and the nightly movements between 0.4 and 3.5 km. On some days the marked elephants returned to virtually the same spot at dusk which they had left at dawn, although the meandering course during the day had covered 4 - 5 km.

BOA F.U. was the most active with a mean daily movement of 2.7 km., compared to M 9's mean daily movement of 2.5 kms, and JEY 1 F.U.'s mean daily movement of 1.2 Kms**.**

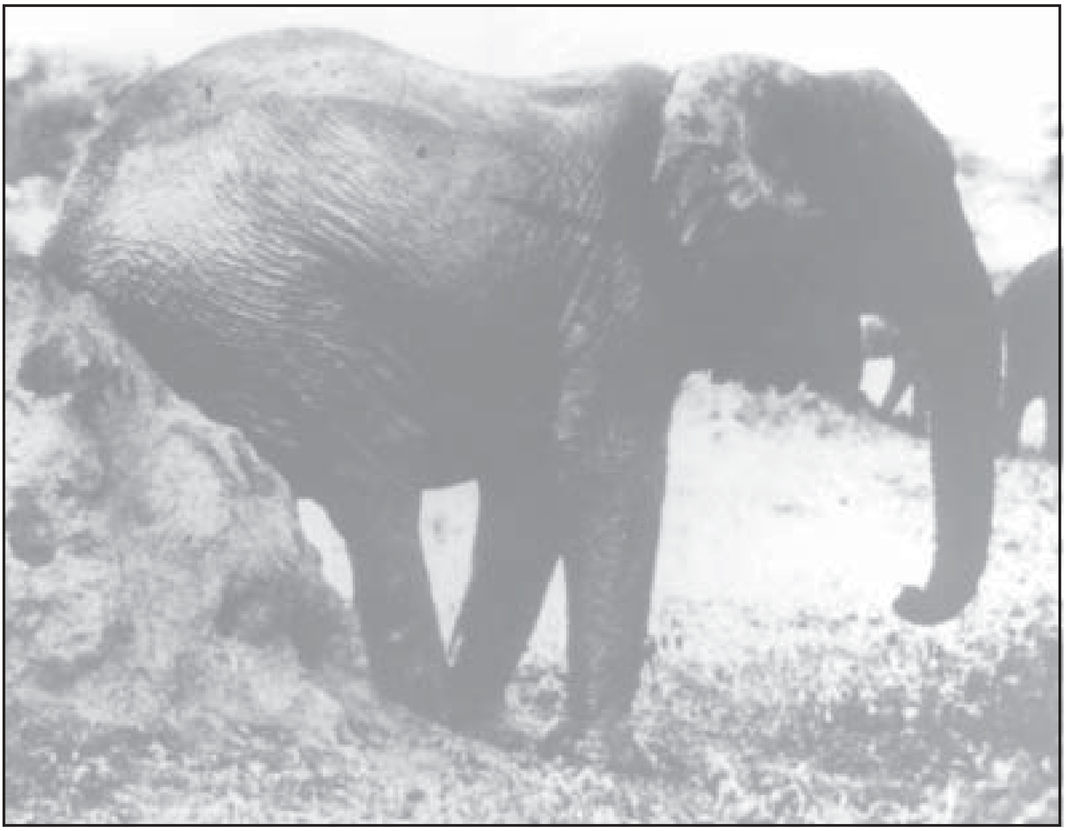
The daily pattern of movement of the radio tracked animals generally resembled that of a feeding assemblage, as exemplified in Figure 5.11. In the morning the elephants were usually found up on the escarpment. Often several groups were strung out within a few hundred metres of each other, with independent bulls scattered between, perhaps spread across a 1–2 kilometre front. The elephants were able to move freely as the escarpment was covered in a network of paths that zigzagged up the hillside, which had been forced through the vegetation and cut into the soil by the frequent passage of elephants. The movements and activities of the bulls and cow/calf groups throughout the day were very similar.

Elephants seen on the escarpment in the morning were almost invariably descending. The time at which they reached the foot of the escarpment depended on the weather. As soon as the sun became hot, usually between 9.00 hours and 11.00 hours, they made for shade. When it was cool, raining or overcast, the elephants would descend much later or even spend the entire day on the exposed hillside. Consequently the tendency to remain on the escarpment or on the plateau above was much stronger throughout the rainy season, particularly after a bout of heavy rain when all the rivers came into spate, (for occupance data see Chapter 4).

Between the escarpment foot and the woodlands or forest was a treeless open zone that runs the length of the Park, rich in herbs, grass and shrubs, through which the elephants passed before reaching the shade. Sometimes they spent a few hours here feeding vigorously. Movements generally followed a stop–go–stop–go pattern both at an individual and at a group level. When individuals were feeding intensively in a given area, each one walked slowly with its trunk probing from right to left among the vegetation. When a suitable plant was located, the animal stopped and fed on it. In small family units most members adjusted their movements to the matriarch's. After feeding in one spot for a time they would then move 50–400 m. relatively fast before slowing down again.

Figure 5.12: Daily activities

A. Wallowing.

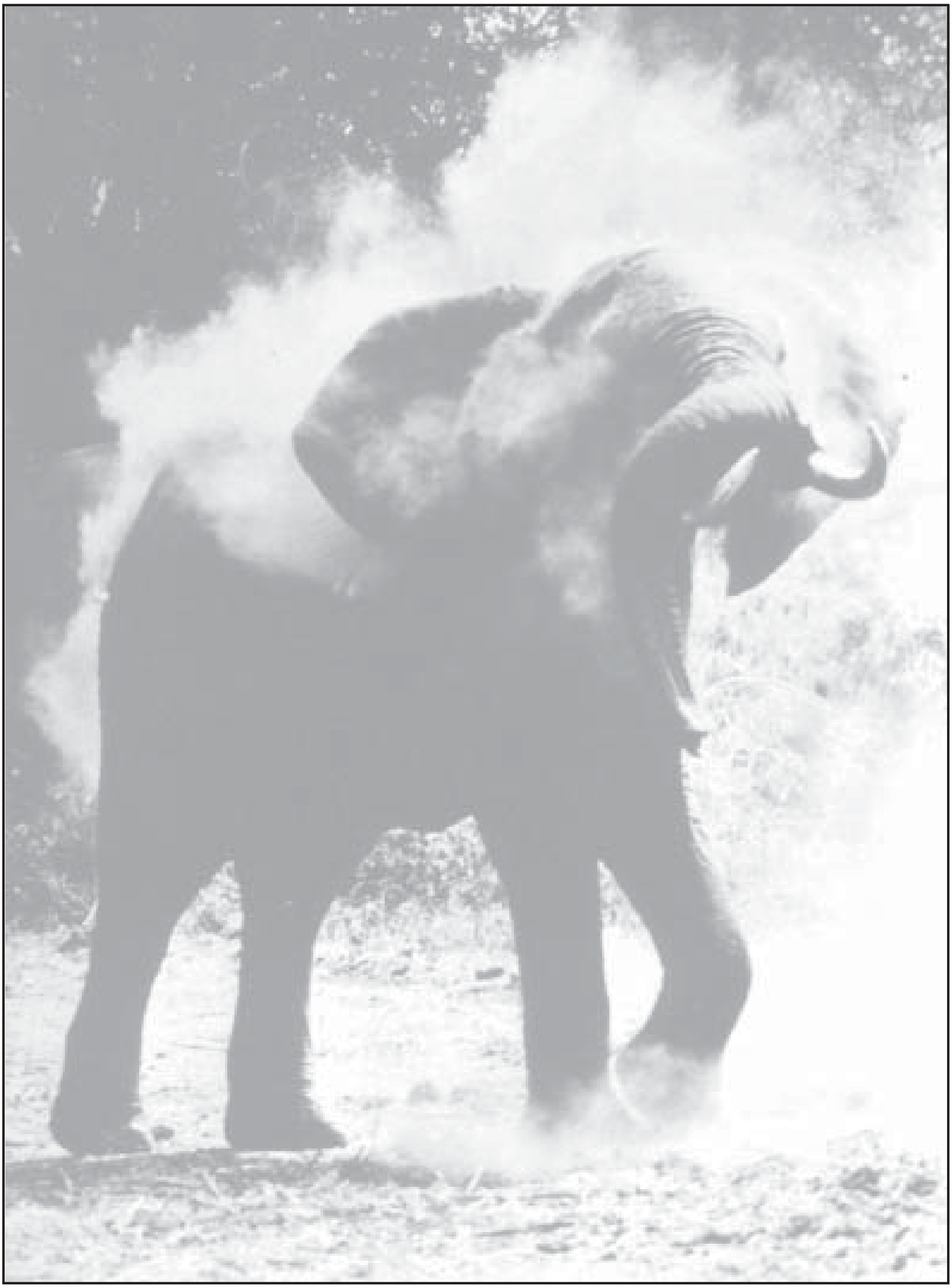


B. Scratching.

Most elephants had entered the woodlands or forests below the escarpment by 11.00 hours and cows and calves usually stayed in the shade until about 16.00 hours. Between these hours they spent much time resting between bouts of feeding. A move to the river, or in the dry season to waterholes, might be made at any hour, but most commonly around noon. After drinking, they usually ‘wallowed in mud pools or swamps, which was followed by scratching, dusting and then feeding was resumed. (Figures 5.12 & 5.13)

In the evenings the groups tended to clump particularly close together and assemblages of ten family units, of the order of 100 animals, were often seen marching from the open shoreline back towards the escarpment in what appeared to be a highly co-ordinated manner. This sort of fast walking was usually only seen in the early morning and late evening, probably because the temperature allowed the elephants to expend energy without overheating. (see Appendix 2 for temperature regulation). At night they tended to climb up the escarpment once more. The mainly nocturnal use of this habitat may partly explain why the escarpment densities censured by air during the day were so low.

Figure 5.13
Daily activities



Dusting.

In addition to the tendency of family units to cluster, there appeared to be a certain synchrony in their movements. In a feeding assemblage, the movement of one group often triggered off movements, in nearby groups. At times a large assemblage of family units moved from one end of the Park to the other. In doing so they were forced to pass through narrow open areas between the escarpment and the Lake. When an assemblage reached a gap in the cover, the family units bunched until they were tightly packed. It seemed that each family was afraid to be the first to become exposed. Then almost together the whole assemblage would begin to move, walking without pause until they had crossed the exposed area and regained cover on the far side. Then once again they dispersed. Figure 5.14 is a photograph of a clumped group of five family units: BOA, LEO, JEZ, SAR and POR, crossing the narrow strip between the Bagayo river and Ndala river.

I conclude that large assemblages form partly because elephants follow a similar diurnal pattern and the limited number of rivers, areas of shade and escarpment impose a restriction on their choice of area, but mainly because family units or males which come into a particular area tend to join and follow the groups which are already there. Superficially it appeared that this process was essentially random, with individual family units and bulls, joining or leaving in no particular pattern. However this was not true, as within the feeding assemblages certain family units consistently appeared near each other and joined or left the assemblage together. This form of association represents the next level of organization in elephant society above the family unit.

Kin groups

I have described how one family unit split with the two fragments later remaining in association, and how within the temporary feeding assemblages, which seldom lasted for longer than 5 days, certain family units tended to be found near to each other more often than to others. BOA, JEZ, LEO (and later ISA when BOA split), showed this tendency very ‘strongly and were usually not more than 100–200 metres apart although occasionally they separated by distances of more than 1 Km. When moving to a mud wallow or water hole they often arrived in quick succession of each other, and at times individuals, particularly juveniles, mixed together in one large conglomerate.

Figure 5.15 shows their movements over a twelve day period in November 1968. Each family is represented by a filled circle. The dotted lines enclose the area occupied by whichever of these families could be located at a particular time.

The spacing of these family units and all others, was analysed for significant long term association in the same way as the bulls’. Since one kilometre had already been defined as the distance at which sub-groups of a family unit lost touch, I scored one association record for any two family units seen separated by less than this distance in one day. Observations were usually made within less than two hours

Figure 5.14
Concentrated feeding assemblage.

Figure 5.15
Spatial relationships of 3 family units BOA, LEO and JEZ over 12 days.

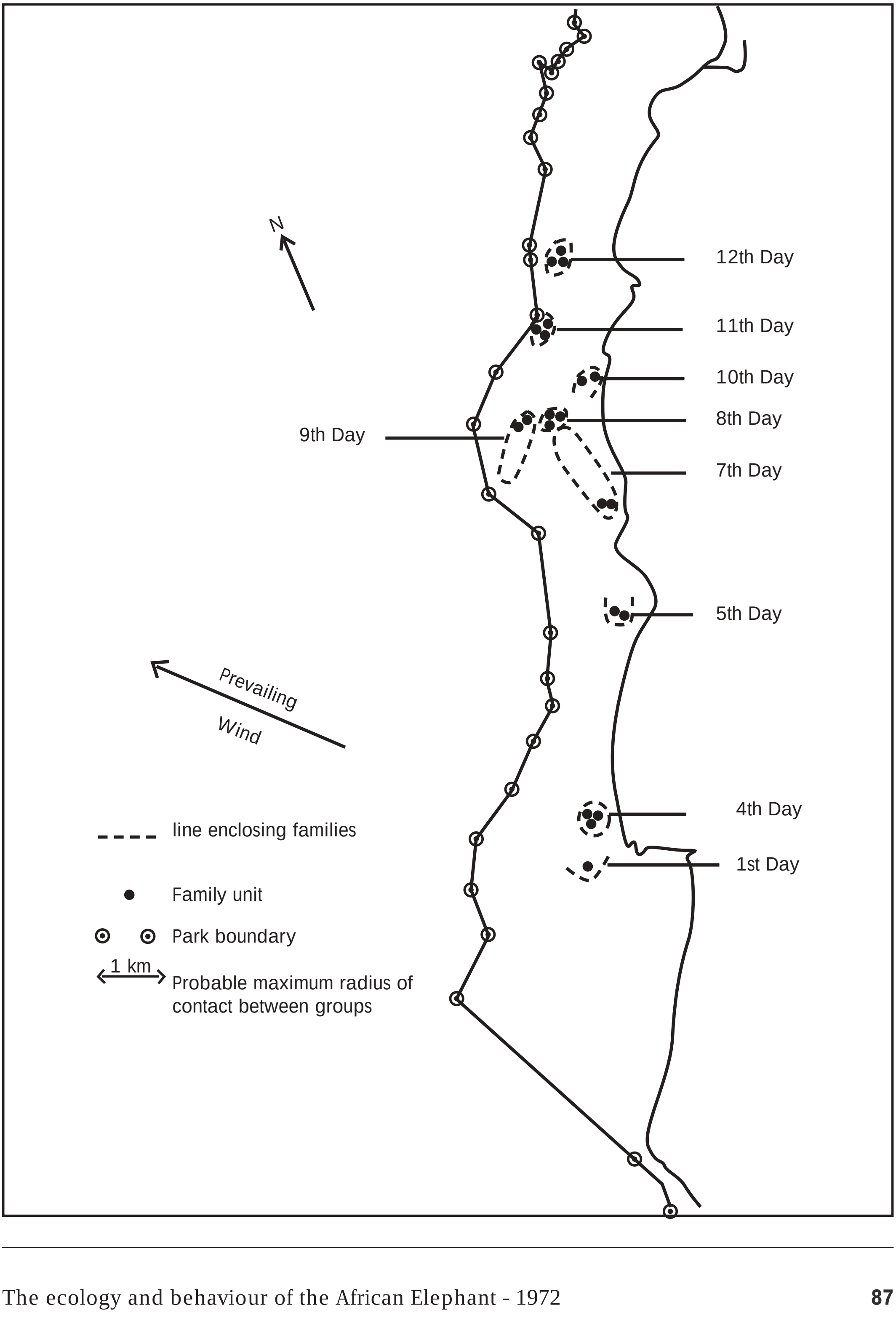
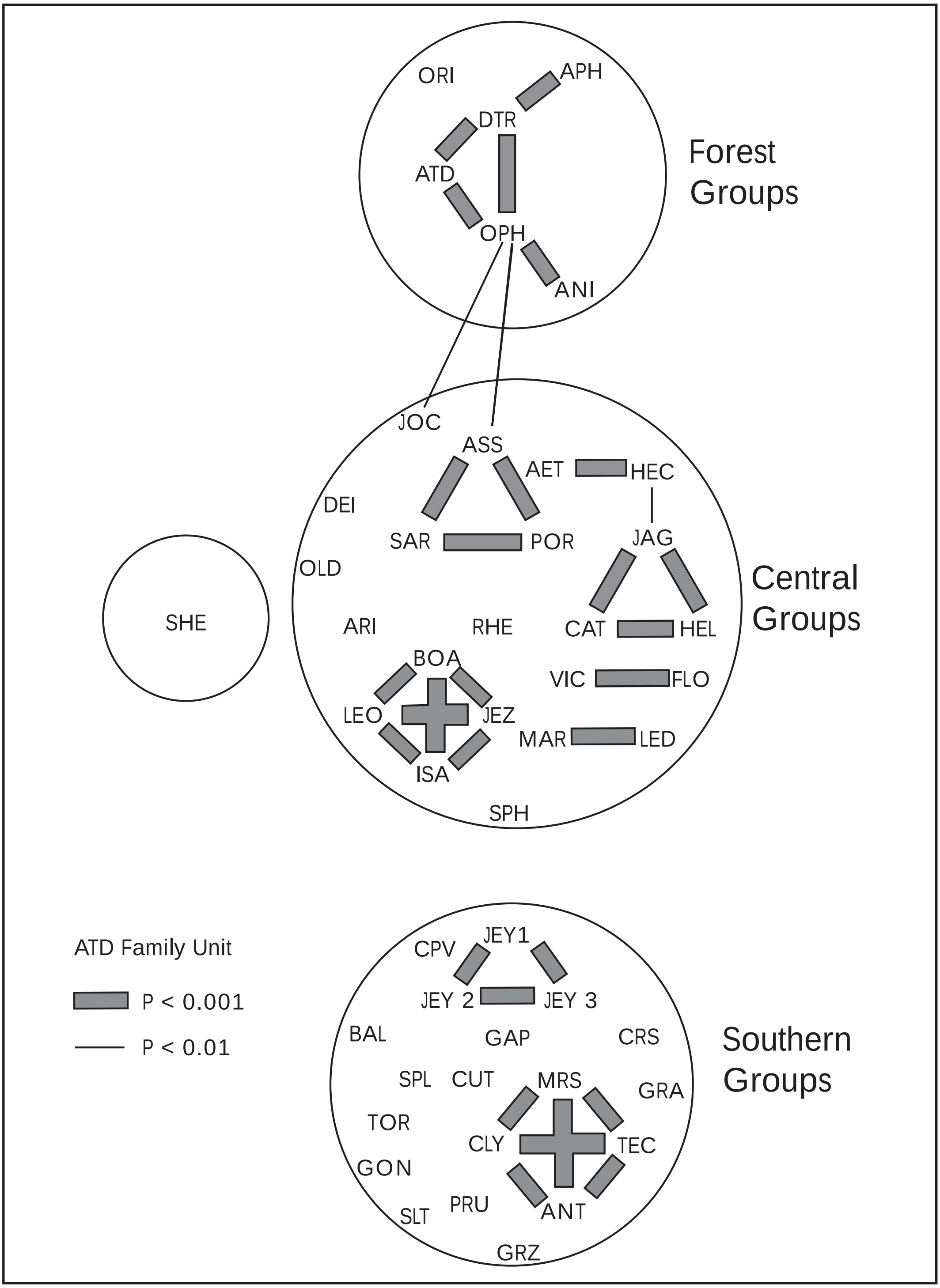


Figure 5.16
Inter-family associations



of each other, but the maximum time difference I allowed was six hours. Over four and a half years I made 4,197 position records of 47 family units. The number of times each family associated with every other one is summarised in Appendix 8.1, and totals 14,274 associations.

Each pair of family units was tested by first calculating an ‘expected’ association value for a random association pattern, and then testing the deviation of the observed from the expected with the statistic X. The results of this analysis are summarized in Figure 5.16. The thin lines joining units represent associations at the 0.01 level of probability and the thick bars at the 0.001 level. The large circles enclose units which shared approximately the same home range.

It will be observed that at the 0.001 probability level, the family units formed associations of doublets, triplets and quadruplets, or remained unattached. With the exception of two pairs belonging to the forest dwelling units, all groups within each configuration larger than two were mutually associated.

Some of these significant associations by this method of analysis could be caused merely by proximity resulting from a shared home range, and the groups which had small home ranges in the Northern Forest may be associated for this reason. The central and southern groups, however, had larger home ranges which overlapped extensively, and I conclude that most of their positive associations were caused by strong inter-group attractions.

As the units within each of these formations remained consistently associated over 4 years, apart from temporary separations of up to three weeks (Appendix 8.2), and as none were seen to leave a formation in one year and associate with a new formation in the next, it is reasonable to conclude that the bonds were long lasting, and probably originated from family units (or extended family units) of about 15–25, which had on occasions exceeded the 1 Km threshold of communications, but which remained consistently associated. This postulate seems more probable than the alternative, which is that unrelated family units, formerly unassociated, joined together to form affinity groups which lasted throughout the study period. Furthermore the gradual increase in spacing observed between sub-units within a family unit, during their development into independent family units, was all part of a continuum, the differences between one level and the next being arbitrarily defined by my 1 Km criterion. Thus I conclude that these higher order associations involving more than one family unit represent true blood relationships. Excluding the forest groups and taking only family units associated at the .001 level, there were 8 formations with a mean size of 28 (range 14 - 48). Their composition in mid-1970 was as follows:

AET	17
HEC	4
	21
BOA	18
ISA	5
JEZ	12
LEO	13
	48
SAR	9
POR	9
ASS	4
	22
VIC	20
FLO	12
	32
CLX	11

CAT	8	ANT	12
JAG	6	MRS	10
HEL	8	TEC	9
	22		**42**
MAR	9	JEY 1	7
LED	5	JEY 2	10
		JEY 3	15
	14		**32**

Table 5.4: Composition and size of kin groups.

Figure 5.17 gives a typical example of spacing within the VIC – FLO formation. It is likely that some of the large cow/calf groups in the South of about 30 each such as TOR, GRZ and BAL were also composed of family units which occasionally split apart, but I lacked sufficient observations to this.

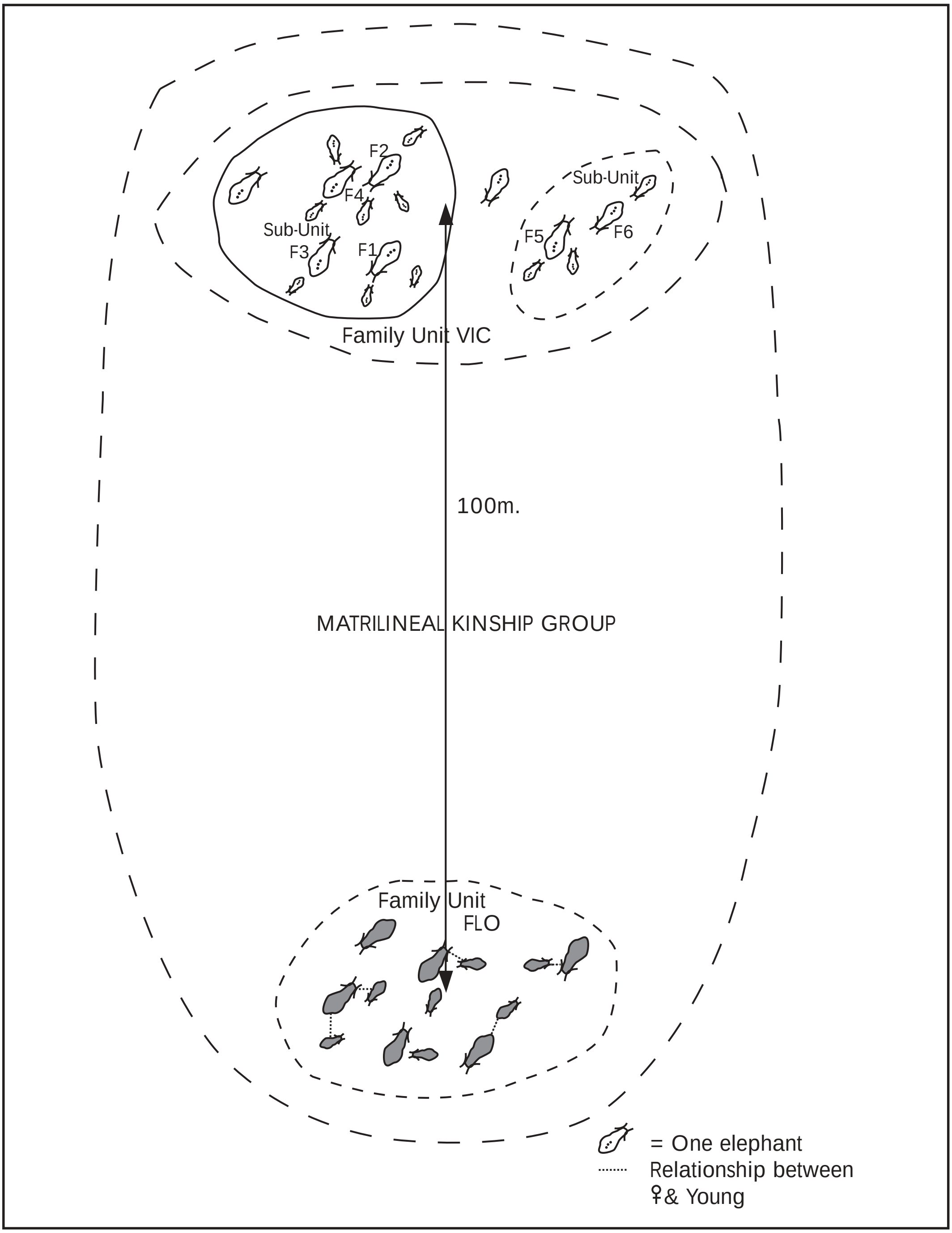
Perhaps the nearest equivalent to these long lasting formations, in size, function and duration of social bonds are certain matrilineal kinship systems of man. In both systems fairly distantly related individuals, are bound by strong social ties, and are found within close proximity of each other in a position to give and receive assistance (as will be shown for elephants in Chapter 6). The elephants need not be aware of their ancestry for the social systems in both species to offer similar advantages to the individual. Likewise the expulsion of the young elephant bulls may have the same effect of preventing inbreeding in elephant groups, as the universal taboos against incest do within human kin groups. (Fox, 1967). The parallels should not be pushed too far, but as no previous description exists of these strong spatiotemporal associations between elephant family units and the relationship implied, the term ‘kin group’ appears to be a suitable descriptive category. The reason for making a distinction between family units and kin groups is that kin groups sometimes split but family units do not.

Amongst the central groups, which could be fairly compared as they were seen so often, the mean size of family units outside kin groups was 14 and within kin groups 10. Three of the single family units, SPH, ARI, JOC, had marked sub-groups giving further evidence of the continuum from one level to the next.

Although social organisations might be expected to differ in areas where elephants have a much larger range there are good reasons for thinking that the kinship system described for Manyara is a basic feature of elephant populations elsewhere. In the Tarangire a young male attached to a family unit was radio-tracked over a period of three months. As the country was relatively open it was possible to count this and other neighbouring groups and to estimate the distances by which they were separated. The family unit with the young male contained two very young calves and usually numbered 11. In 12 out of 22 observations a second family numbering 12 was seen within less than 200–300 metres, which could be identified by a large female with only one tusk, on the right. On two occasions these two groups were seen amalgamated numbering 23, and on three occasions the tagged group was seen within a large cluster of groups similar to the feeding assemblages seen from the air at Manyara. As the area covered and rates of movement were much higher than at Manyara, the association between the two families was all the more remarkable and

Figure 5.17

Typical spacing of individuals in VIC (plain) and FLO (Black) F.U.'s in 1968, all members of one kinship group. A pubertal male stands between sub-units of VIC F.U. (Compare Fig. 5.6)



I conclude that they both belonged to the same kin group.

Furthermore the populations of Murchison and Tsavo showed modal points in their group size frequency distribution, and it was suggested that larger units were essentially aggregations of family units and bulls (Laws & Parker, 1968; Laws, 1969b: Laws et. al. 1970). The Manyara evidence supports this conclusion, but modifies the further suggestion that "the sizes of groups above about fifteen are determined by an essentially random process of individual family units or bull herds joining or leaving") Laws & Parker, 1968). I suggest that groups of 15–50 seen from the air may occasionally be random aggregations, but are more likely to consist of two or more family units belonging to the same kin group.

Observations of the Indian elephant Elephas maximus, suggest a similar organisation. Mackay (1971) described groups of less than 15 similar to the family units of the African elephant, and "herds" numbering 15 - 80 animals composed of several "family groups". Although "herd" ranges overlapped, cut of 120 observations of groups he never saw any transfer of individuals from one "herd" to another. This evidence although inconclusive suggests that his "herds" may also be composed of related animals.

It is possible that even larger groups may be consistently associated, and may even be related as 'clans' of 100–250 animals. (Laws, 1969b).

A slightly different method of analysis of the Manyara family unit association matrix (Appendix 8.1), using a X^2 test of association (Southwood, 1966), showed three large divisions within the population, which numbered 3, 22 and 11 family units each; corresponding to the Forest, Central, and Southern ranges respectively. The results of this analysis are summarized in Appendix 8.3. At this level the problem of whether shared home ranges caused the associations, or whether blood relationships caused the common home ranges cannot be answered. However, the lack of cross-associations from one range division to the next is suggestive of some 'clan' level of organisation. Only a lifetime of monitoring could produce a definite answer.

Home Ranges

The home range of each bull and family unit was delineated by drawing a line around the outside of all its position records. Figure 5.18 represents the home ranges of four different family units and one adult bull selected to illustrate variations in size and shape. It will be noted that ORI and APH F.Us were seen mainly in the Northern Forest, but that they overlapped with BOA F.U., that occupied a large central range, which in turn overlapped with JEY F.U., a group that lived mainly in the South. Where radio-tracking studies were made, the movements have been indicated and it can be seen that both for BOA F.U. and JEY F.U. this method allowed ranges to be plotted even in the Southern Endabash thickets.

Altogether 73 home range maps were compiled, 48 for the cow/calf groups, and 25 for the most commonly seen bulls. (For Number of sightings per group see Fig. 4.4). Routine sightings, confirmed by the three radio tracking studies, showed that each group covered most of its range every month, although the probability of sighting them in certain habitats varied seasonally. The ranges of most groups, extended in width from the Lake shore up to the escarpment heights two or three kilometres inland, and in length ran for about 15 Kms. along the long axis of the Park. As each group ranged approximately equally far inland, home ranges can be represented in linear form, on an approximately North - South axis. I have attempted to summarize the range and amount of time spent by each group in different parts of the Park, by separating the Park into four roughly equal areas, and dividing the number of sightings of each group in each area by the number of patrols that I made in that area. The correction is approximate as no allowances were made for visibility differences between habitat, but differences between groups should be valid. The corrected values have been adjusted to the same scale, and appear in Figs. 5.19 and 5.20 as approximate histograms of the proportion of time spent by each group and bull in the four different sections of the Park. The units are arranged in the order of their range preference along the North–South axis. ORI F.U. had the smallest range, which was 14 Km^2. in area and 5 Km. in length. In contrast, BOA F.U. had the largest range of 52 Km^2. in area and 26 Km. in length, but even this group did not use all the Park and was never observed either in the extreme North or South.

All home ranges overlapped extensively with others. 15 family units and eight bulls had ranges which overlapped with the ranges of all other elephants sighted in the study period. Even ORI F.U.'s range overlapped with 28 others. It was clear that there were no mutually exclusive parcels of territory. Rather there was a continuum of ranges from the forest dwellers in the North down to the southernmost family units. Behaviour did not show territorial tendencies either. Nonetheless, there were great differences in the position of ranges, in their sizes and in the relative amounts of time that each family unit spent within the different portions of its range.

ORI and APH F.U. s, the two groups which were most restricted in range to the Northern Forest were anomalous in the proportion of times they were seen in association with other groups, both. tending to be seen alone more often than not. In part the scarcity of association records of these two groups may be due to low visibility in the Forest, and in Table 5.5 below, the forest family units have been placed in the order of their range preference in the north - south axis:

Table 5.5: Associations of Forest Units

	Times seen Associated	Times seen Alone	% Alone
ORI	13	15	54
APH	20	53	71
DTR	49	29	37
ATD	42	16	28
0PH	57	32	35
ANI	91	39	30

Figure 5.18
Manyara family unit home ranges and one bull.

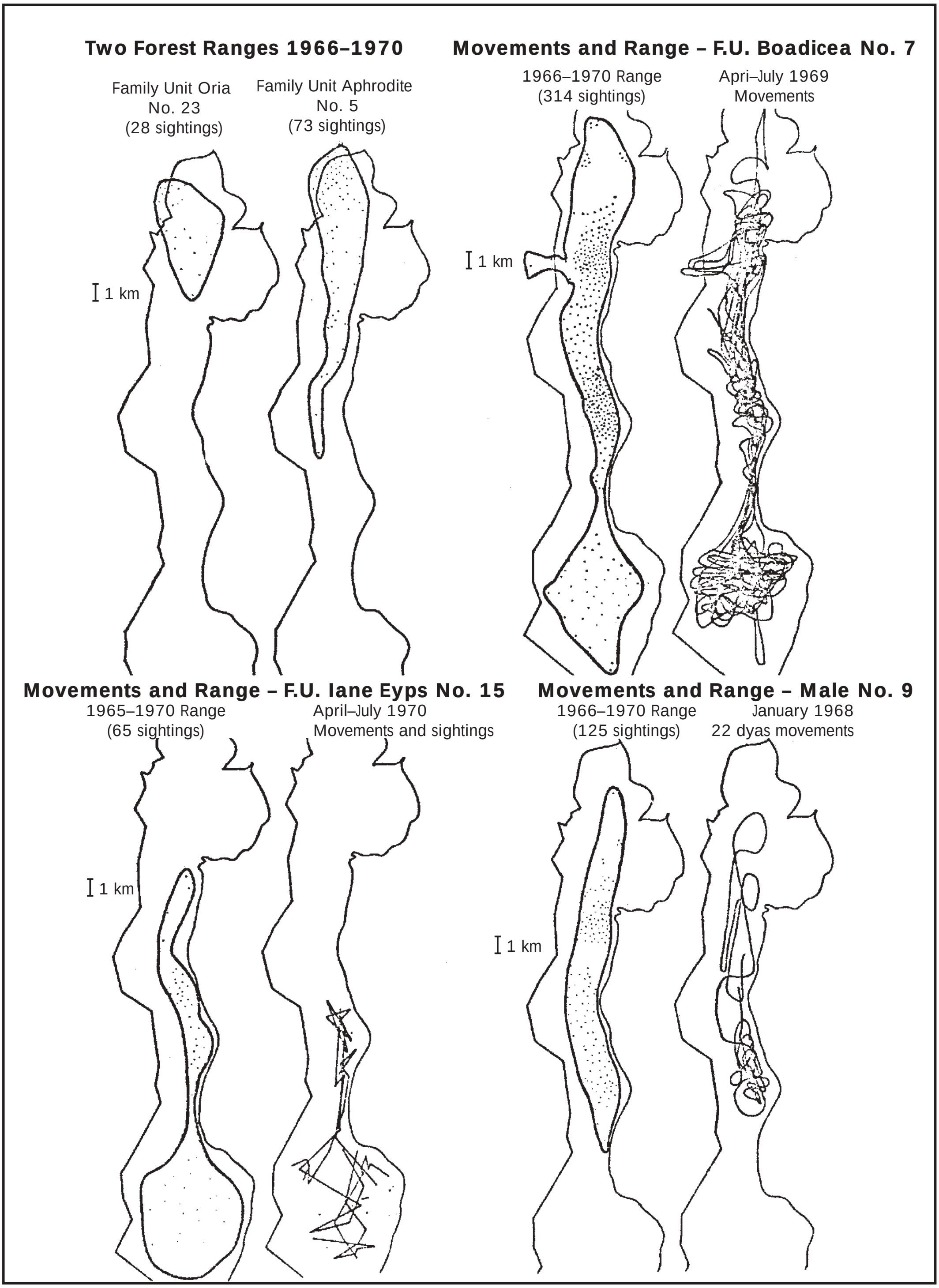


Figure 5.19
Family unit range utilization.

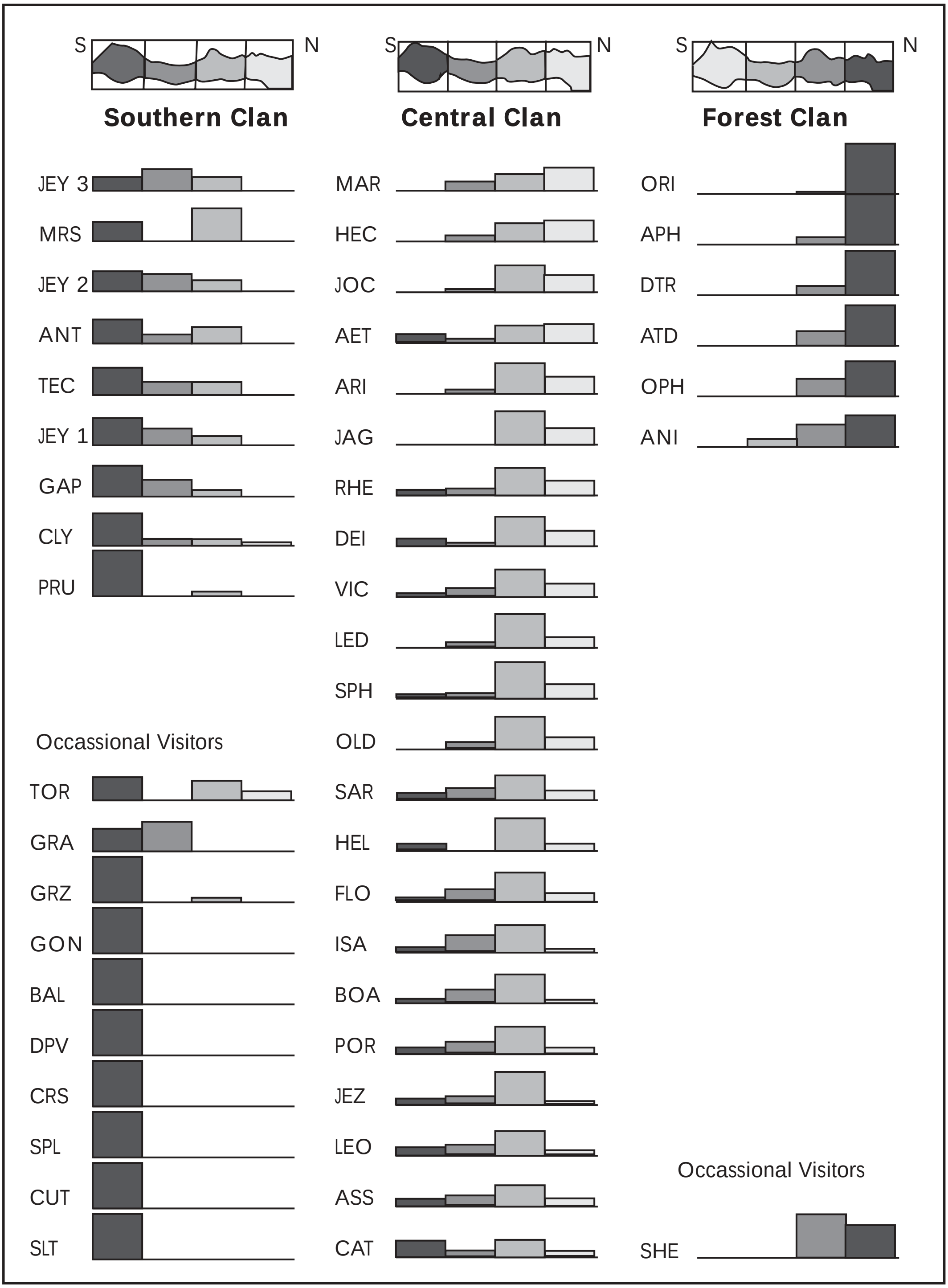
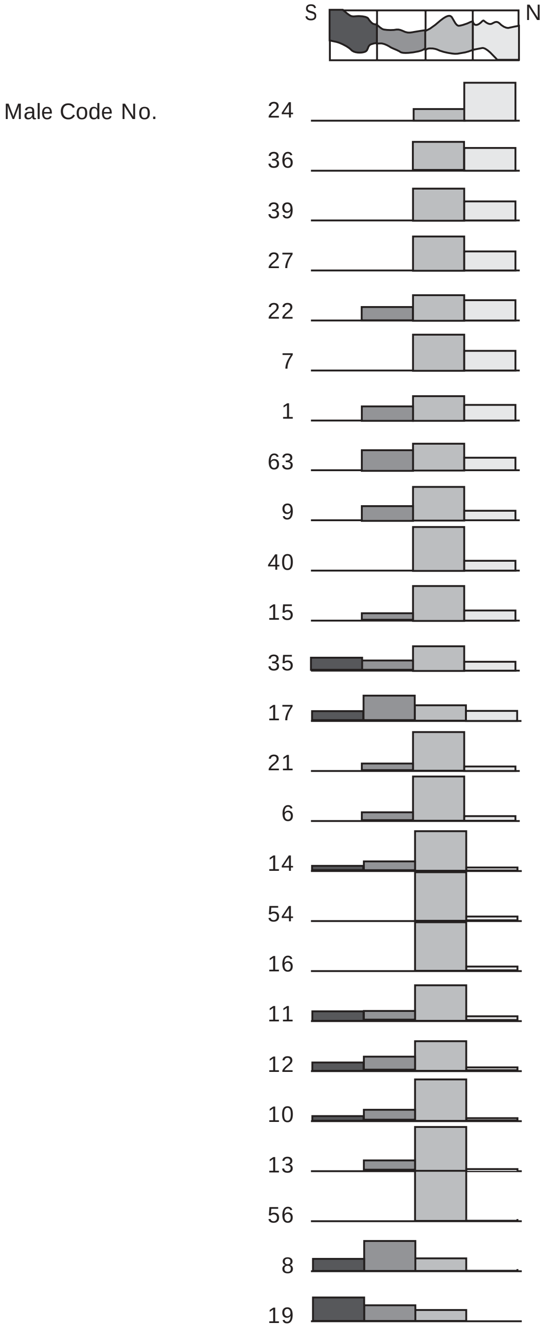


Figure 5.20
Male range utilization.



An approximate histogram is given for each of the 25 most commonly seen bulls of the amount of time it spent in four sections of the L.M.N.P.

The differences were shown to be significant ($X^2 = 44.3$, df. 5, $p < .001$). The possibility that these two groups actively avoided others cannot be discounted, particularly since they have been shown to have relatively small ranges, which might be a result of this tendency. However, their ranges were almost certainly larger extending into the Mto-wa-Mbu forest before it was cut down in the 1960's (Fig. 2.5)

When the Manyara home ranges are compared with minimum ranges of individual elephants in other areas (Fig. 5.2 1, the extent to which these Manyara elephants have been restricted becomes apparent. Although a high food availability or social factors may partially cause small range size, it is certain that the elephants would range much further, as they did in former years, but for the surrounding human settlement.

Some elephants still used areas outside the Park. Five Manyara bulls were seen on three separate occasions 15 miles north of Mto–wa–Mbu village in the Kitete Chini patch of forest. From here they may have easily made their way up a well known trail that climbs the escarpment into the 896 Km^2 (350 square miles) Ngorongoro Forest Reserve. (Fosbrooke, 1972). The 22 central F.U.S seldom if ever left the Park except up the Musasa River Gorge, which only extended 2 km. outside the Park or on the escarpment above the main Mto–wa–Mbu–Karatu road.

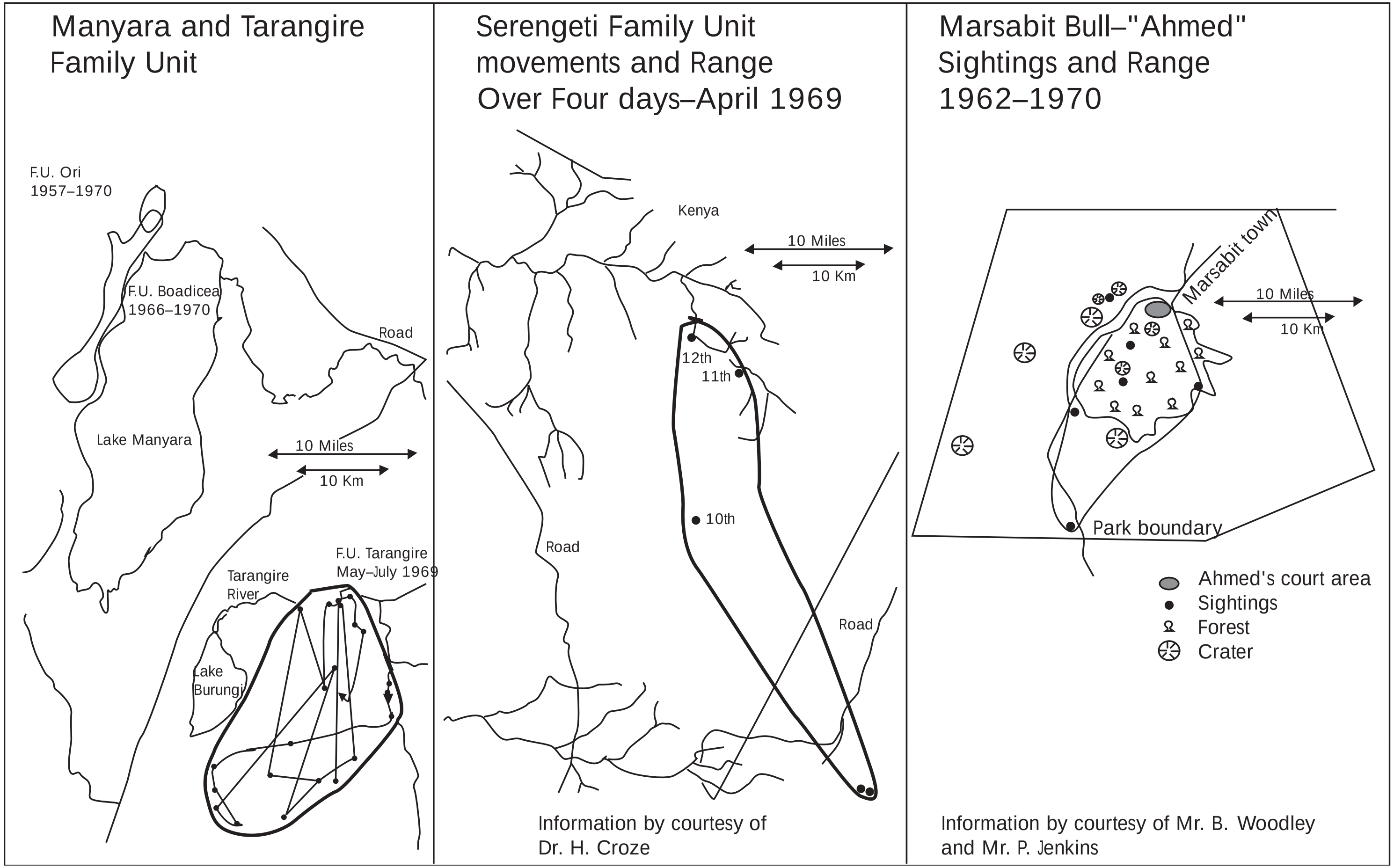
One group, however, did not fit into the general pattern; this was SHE F.U., I only saw it over two periods, one in 1966 and the other in 1968, each of which lasted about a week, in the centre of the Park. The family had about eight members and the matriarch was very distinctive with larger tusks than any other cow in the Park. The group was very tame and I could approach it closely. The last time I saw them was outside the Park along the Musasa River Gorge. I believe that they came from the Ngorongoro Conservation Area, their tameness being attributable to the protected status of that area. They probably crossed over at night, moving through the farms until they reached the Musasa River Gorge. The size of the matriarch's tusks suggested that she must have been very old, and may have memorised the route in the days before the second World War, when according to local residents elephants commonly passed from Ngorongoro to Manyara.

The family units which I assumed to live permanently in the south were often overlooked during a quarter (Fig 4.4), but I believe that they were permanently resident, as when JEY 1 F.U. was radio-tracked from April to July 1970 this group never left the Park, but remained mainly in the dense Endabash area. It also became obvious that this family unit was part of a kinship group and the two other associated families were named JEY 2 and JEY 3.

There were also a further ten families in the south seen so seldom that I assumed that they were only occasional visitors.

I conclude that there is some slight evidence from common home ranges and observed associations that family units may be grouped as clans, and that at

Figure 5.21
Minimum home ranges drawn to the same scale, of individual elephants or family units in four different areas of Tanzania and Kenya.



Manyara and Tarangire Family Unit

Serengeti Family Unit movements and Range Over Four days–April 1969

Marsabit Bull–"Ahmed" Sightings and Range 1962–1970

Information by courtesy of Dr. H. Croze

Information by courtesy of Mr. B. Woodley and Mr. P. Jenkins

Manyara there were possibly three clan ranges, which in 1970 numbered:

5–6	family units living mainly in the Northern Forest.
22–23	family units living mainly in the Centre.
9	family units living permanently in the South.
10	family units occasionally visiting the Park from the South, using the South as part of their range.
11	family unit occasionally visiting the Park from the West.

Meetings between strange Family Units

In view of the possibility that territorial mechanisms may operate at family unit or clan level as suggested by Laws & Parker (1968) and Laws (1969a), it was of great interest to observe the interactions of family units from the different "clans" at Manyara when they came into the same area.

On the 37 occasions when Aphrodite and her family came into contact with the central groups (i.e. within 1 km.). I never observed any unusual spacing or interactions between her and the other. On several occasions she joined a feeding assemblage frequently coming within less than 50 m. of other F.U.s, and in one instance intermingled amicably with JOCF.U. If her relative isolation was the result of the presence of other elephants south of her range, then it was caused by her avoidance of them, rather than acts of aggression on their part.

Likewise groups from the south did not appear to elicit hostility from central elephants when they met where their ranges overlapped. TOR F.U., a large group of about 30 animals which occasionally visited the Park, once passed straight through an assemblage of six F.U.s, all central groups, with no aggressive interaction. The tendency of strange family units was to join the feeding assemblage 'within an area and remain closely co-ordinated for a few days. Hostile interactions between different elephants are found in other contexts which will be discussed in the next Chapter.

CHAPTER 6 — SOCIAL INTERACTIONS

SOCIAL INTERACTIONS

Introduction

In the previous chapter the social organization of elephants was described at several different levels, in terms of range, spacing, and relative stability of the different social groups. Returning to the central problem of the thesis, the social interactions must now be examined as possible determinants of elephant population regulation. The overlapping of the home ranges and lack of territorial defence, described in the last chapter, suggest that reproduction is not influenced by any territorial process, but the question remains "is there any other social behaviour in elephants directly related to density which might affect the individual's reproductive rate or chances of survival?"

In this chapter social interactions will be reviewed and their adaptive significance discussed. In particular, care of the young, social aggression, co-operative and sexual behaviour will be examined in relation to density or other environmental variables, which themselves might be related to density.

Essential to an understanding of elephant social interactions is some knowledge of their means of communication.

Communication

Throughout my study I paid attention to the ways in which the elephants communicated. My priorities did not allow experiments, but by careful recording of many isolated incidents I could get a fair impression of the manifold types of signalling the elephants employ. In the following account I shall attempt to present information on both motivational and functional aspects of what I consider to be the elephants' communicatory repertoire.

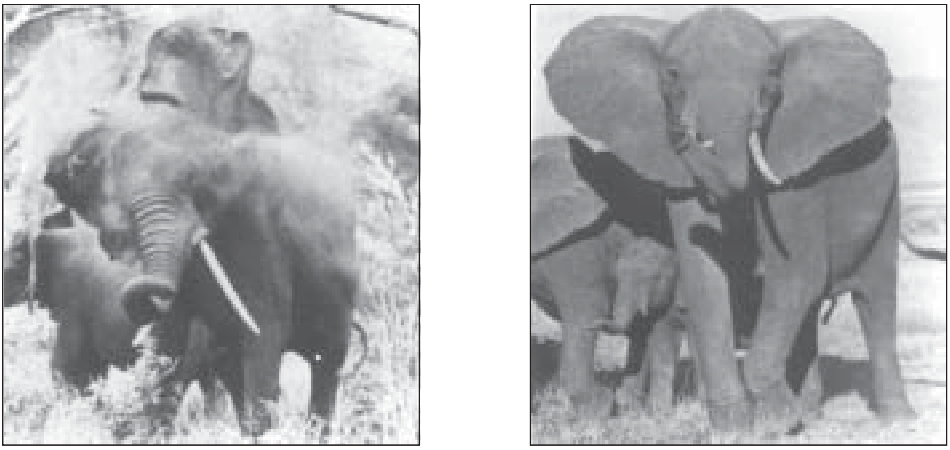
Available Senses and Sensitivity

Elephants appear to communicate by sight, sound, smell, touch and taste. Of these senses smell and taste are the most difficult to observe, although they are perhaps the most important to the elephant.

Corresponding to human perceptual ability I recorded most behaviour in visual terms, (giving motivational interpretations to various postures, and social interactions). From sniffing movements of the trunk and the sucking of the trunk tip, I made deductions about the role that olfaction and taste played in their behaviour. Vocalizations and other noises made were recorded qualitatively.

Figure 6.1
Threat displays.

A. **Head toss I** **B.** **Head toss II**



C. **Head shake** **D.** **Head swish**

C. **Stand tall**

Vision

However poor the elephant's distance vision may be, experiments on tame Indian elephants have shown that at close range an individual's vision is acute enough to perceive and discriminate between more than 40 different angular and curved shapes and patterns (Rensch, 1957). Altevogt is quoted as proving experiment that the visual ability of the elephant is about equal to that of the goat and the deer (Rensch, 1957). There is no literature indicating that the African elephant is inferior in its visual perception.

Any deduction in the field about elephants' vision must be made from observations where hearing and olfaction can be ruled out as stimuli. If an elephant has not been previously alerted by sound or smell, a man moving slowly in a bushy habitat is usually able to approach it within 10 metres without being seen. In situations where the object is sharply contrasted with its surroundings their visual perception is remarkably improved. Movement also attracts their attention. For example, a man walking on a white sandy riverbed and wearing dark clothes may be spotted and recognized at 200 metres, whereas a buffalo under similar conditions would be ignored.

From the reactions of groups that I have approached I gradually gained the impression that young animals use eyesight more than older animals. If this is true it may be because they tend to hold their heads higher, with the axis of their vision nearer to the horizontal than the adults, which when undisturbed usually have their heads and eyes down. Nonetheless elephants do frequently look up and I have been spotted high above their heads in a tree on several occasions when I moved inadvertently. Their field of vision extends far backwards. As they retreat they are able to look backwards at the source of disturbance and respond rapidly to any further movements. They are also very well aware of movements around their hind legs, and a strange calf may sometimes be pushed or kicked away by the very precisely directed back legs of an adult.

Like many other mammals, elephants have a reflective layer "tapetum" in the retina, which at night can be seen in the head-lights of a car. Judging by these reflections the reflectivity lies between that of the Carnivora and the human species. This suggests that their eyes are adapted to nocturnal vision to a certain extent.

It appears therefore that at the ranges at which social interactions take place i.e. 1-50 metres, the elephant could potentially transmit and receive information by means of postural signalling. The elephant's powers of visual discrimination and the variations provided by trunk, head and ear attitudes, would allow for a high degree of complexity in the information content.

Threat postures

The extent to which various postures have developed a signal function is difficult to assess. An ethogram of postures relating to social aggression and 'fear' has been constructed by Kühme (1961), working with three captive African elephants. He attached significance to head, ear and trunk postures. Among wild elephants the most stereotyped movements occur in threat and when the animals are alarmed. As the threat postures are similar both in inter and intraspecific contexts they are described here, and classified as follows:

Ear extension:	the ears are held tensely forward, or flapped.
Head nodding:	a rapid up and down motion of the head usually seen when walking.
Head jerk:	a small single rapid upward movement of the head which then returns down slowly.
Head toss:	a pronounced version of the head jerk in which the head is first lowered and then pulled up so that the tusks describe a wide arc.
Head shake:	the head is twisted to one side and then rapidly rotated from side to side. The ears usually slap against the side of the face making a loud smacking noise.
Stand tall:	the head is held high with the ears maximally forward. The animal appears to increase in height and sometimes wall deliberately stand upon an object such as a log (Fi 6. 1 E), or ant heap in order to increase its height.

Some of these postures are illustrated in Fig 6.I opposite.

The trunk is capable of an almost infinite variety of postures. Fig. 6.2 shows resting postures which presumably have no signal function. A large number appear in aggressive behaviour see Fig. 6.3, but also in other contexts. *A* relatively stereotyped form is the forward trunk swish, in the direction of the opponent (Fig. 6.1). This gesture is usually employed by elephants against smaller opponents. One cow, Boadicea, sometimes threw objects at vehicles. Kühme (1961) relates the end posture of a trunk swish to maximal aggression in elephants, but a similar posture is also seen when the animals are investigating, or when they meet. Both trunk and ear movements appear in different combinations with the head movements. The tail also appears to indicate the mood and is raised when an elephant becomes excited both when aggressive or when alarmed. While I have no proof, I had the impression that some of these 'expressions of the emotions' (Darwin, 1872) have a signal function, and movements and postures will be further described and discussed in the behavioural contexts in which they occur.

Hearing

Estimates in the literature of an elephant's powers of hearing range from very acute (Sikes, 1971) to moderate.

Benedict (1936) recorded that a circus elephant responded to the quiet voice of its master even in the midst of clatter and

Figure 6.2
Trunk postures at rest.

noise. Rensch (1957) wrote that fully trained captive Indian elephants were able to distinguish between and respond to 24 different verbal commands of their mahouts. The training of the sub-species Loxodonta cyclotis in the Congo suggests that African elephants have a similar auditory discrimination (La Plume, 1911).

My own conclusion, based on the reactions of elephants to noises which I have made when approaching them, is that their hearing is equivalent to that of an above average human being.

Vocalization; and other elephant noises

The vocalizations of elephants include a wide range of growls, trumpets, squeals and shrieks. Each of these sounds may vary in frequency, amplitude, duration and the sequence in which they occur. Many other sounds are generated more indirectly during; feeding, drinking and wallowing. Branches may be broken and water or mud noisily splashed around. Clearly the auditory channel of communication has a high information potential. I have classified these vocalizations and their possible functions as follows:

Growling

The growl is a deep sound like a rolling ‘r’. It is one of the commonest vocalizations and appears in many different behavioural contexts. It has often been referred to as a tummy rumble (e.g. Fitzsimons, 1920), but is in fact generated laryngeally (Buss, 1962). This sound can carry up to nearly one kilometer.

Members of an undisturbed feeding group usually emit gentle growls at intervals. When an individual has drifted away from the others it growls loudly and this seems to act as a signal, for it usually evokes a similar response from a fellow member of the family, who is most often the largest female or matriarch. At times it is used when other families are nearby and appears to serve the same contact-promoting function, with one family calling and the others within earshot answering.

> In several examples I saw behaviour which suggested that elephants can recognise the individual call of other members of their family. For instance, one evening in December 1967, within a co-ordinated assemblage of about 100 elephants, composed of eight intermingled family units that had clumped together, members of one group, SPH F.U., became separated from each other. The whole concentration of elephants was moving across an open patch of ground and at its head was the matriarch Sphinx, of SPH F.U. The second female of this group, Avia, had drifted to the tail of the concourse with her new-born calf, and appeared to be extremely agitated.

Avia emitted a loud growl and was immediately answered by Sphinx. Avia straight away increased her pace and hurried through the files of other elephants

Figure 6.3

Trunk postures in aggression (in sequence)**.**

A young bull at left threatens a larger cow at right by spreading his ears. These trunk postures are not only found in aggression.

until she rejoined her own family. All members of SPH F.U. then clustered tightly together growling and milling around.

Growling is characteristic of meeting behaviour and is almost invariably used together with trunk contact and other forms of tactile intercourse (see below) when members of a F.U. or kin group reunite after temporary separation.

Other mammals employ similar contact calls, such as reindeer where each mother recognises her young by its individual call out of hundreds of bleating calves (Espmark, 1971).

The tonal quality of the growl can be altered by the extent to which the mouth is opened. With the mouth wide open the growl becomes a bellow, which is often emitted when an elephant is suddenly attacked by another. It also appears in other situations where the elephant can be presumed to experience pain, such as if trips and falls or bangs into a rock when running away. I have also observed an elephant of about eight years, growling repeatedly while the rest its family unit behaved normally. Its incessant circular walking and disturbed manner, while the others grazed and browsed peacefully suggested that the animal might be suffering some internal pain. Its associates paid no attention to it and I watched it for about an hour. Lang (1967) describes a young cows moaning, while giving birth, which is presumably a variation of the growl.

In competitive situations the growl acquires an aggressive significance, particularly between cows and calves when the calves try to push into waterholes dug in the sand by their mothers and during play fighting. The volume of the growling here is indicative of the level of arousal, and a loud growl from the mother is likely to be followed by a sudden thrust of the tusk or trunk.

Growling is also characteristic of interspecific threat displays. When the elephant is fully aroused the volume becomes greatly increased and it is better described as a roar. Combined with trumpeting it forms part of the whole threat complex described later.

Growling also appears to have a soothing effect on disturbed young animals when emitted by an older cow in a moment of stress (see below). It is possible to detect qualitative differences between several of these different types of growl, which in the absence of recordings defy objective description.

Trumpeting

Trumpeting is produced by a forcible exhalation which resonates within the trunk as if it were an organ pipe. The trunk is usually held straight down or slightly curving backwards. Trumpets may vary in duration from a sudden blast produced when an animal is startled to a prolonged note accompanying a full threat display. At a much lower intensity air may be rapidly exhaled making a ‘whooshing’ sound. There are also a variety of respiratory noises, apparently bronchial in origin, commonly emitted by feeding elephants, which do not seem to have any specific communication function,

Trumpeting is primarily used in aggressive situations and may be employed by elephants both among themselves or against other species, although when very excited it may appear when members of a family unit meet after separation.

Squealing and Shrieking

Baby elephants have a distress squeal which provokes an immediate response from their mothers and other cows (see below). In the adult the squeal becomes a shriek or scream which may be used together with growls and bellows in agonistic situations, or in interspecific threat displays.

Olfaction and Taste

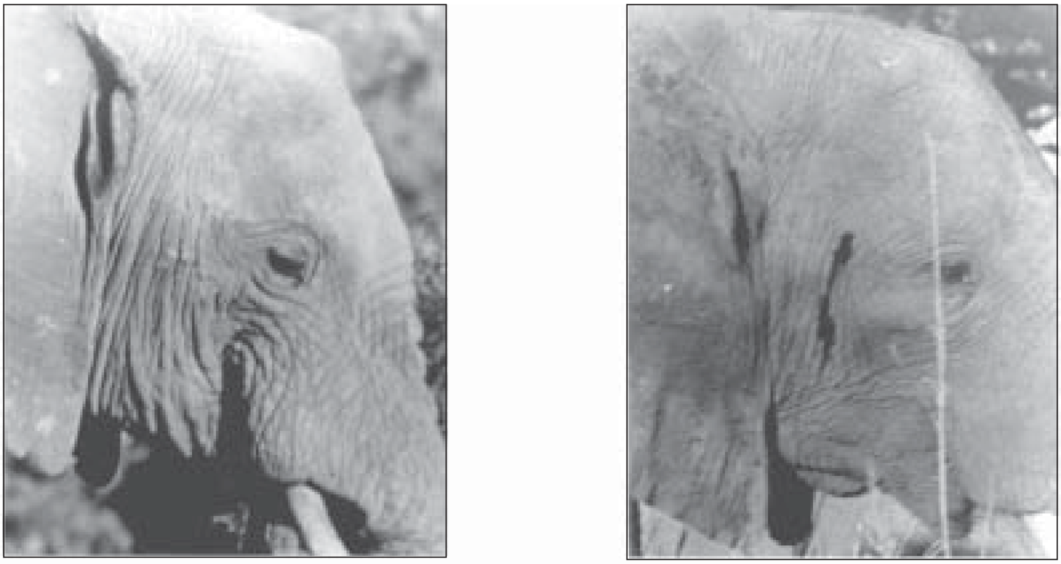
The sense of smell is particularly well developed. The trunk is shifted to sample air currents in different positions which must greatly increase its olfactory efficiency. The characteristic moving of trunks is often the first visible sign that a group is aware of a human intruder's presence. I have seen elephants react to my presence when I have been more than half a kilometer upwind. The well developed hairs near the tip of the trunk may have a tactile function in detecting slight wind pressures in order to inform the elephant of the precise bearing of the scent.

Elephants can also follow a cold scent trail and I have seen a separated individual track its Family Unit by putting its trunk to the ground and following the exact paths where the members had passed two hours previously. Elephants have also been reported to track human antagonists in a similar fashion (Lamprey pers. Comm..). Under exceptional conditions of ground humidity a bloodhound can follow the scent trail of a man when it is over 48 hours cold and can pick the right man out of twenty others using olfaction alone. (pers. Obs.). It seems to me probable that an elephant's olfaction is equal to or better than a bloodhound and scent tracking may well be one of the most important means by which a family or 'kinship group' maintains its cohesion. A trail would last much longer if elephants deliberately scent-marked as they walked along. Scents in other species, such as dwarf mongoose (Dr. A. Rasa, pers. Comm.) and cats, have been demonstrated to elicit a response more than 20 days after deposition.

Scents, 'scent-Marking', and Taste

The only scents that I was able to detect, which evidently had a communicatory function, derived from the temporal or 'musth' gland, the urine and the faeces; although the tracking ability suggests the possibility of interdigital glands. The temporal gland is apocrine (short, et. al. 1967) and is situated between the ear and the eye. At intervals it secretes a strongly smelling viscous substance. This may trickle down the side of the face making a dark smear (Fig. 6.4). It may also reach the corners of the mouth, possibly stimulating the sense of taste.

Figure 6.4
Musth gland secretion.



A. None **B. Slight**

C. Moderate **D. Strong**

It is difficult to describe, without some hesitation, any elephant behaviour definitely as scent marking. I can confirm that the temporal gland is frequently rubbed on the side of trees (Sikes, 1971), and on the ground particularly in the vicinity of mud wallows, when elephants lie on their sides and roll, but these activities are usually seen in relation to general body scratching which includes all parts of the body. Although elephants may sniff the anus, ureno-genital aperture or musth gland (see below), I did not form the impression that these organs were rubbed more frequently than the back, flanks, neck, belly, fore and rear quarters. However, a strong smell of elephant could usually be detected around a recently used mud wallow or tree trunk.

The incidence of musth gland secretion in the Manyara population was not related in any obvious way to time of day, season, sexual activity, or to any particular adult male, female, or family unit according to its position in the social hierarchy.

Musth secretion did appear to be related to age, gender, excitement and possibly to elephant density. The Table 6.1 below shows the relationship of temporal glandular activity to age and sex in the adults. Both wet and dry season data over six months in 1969 are pooled.

Table 6.1
Age groups

	0–1 yr	2–3 yrs	6–10 yrs	11–15 yrs	Adult Female	Adult Male
% with Temporal Secretion	0	43	59	83	90	54
Sample Size	7	42	32	19	210	210

The gland only begins to secrete after the first years of life and an increasing proportion of animals show the secretion in the successive age classes. 90 per cent of adult females were observed secreting compared to 54 per cent of the mature bulls, a significant difference. (X^2 = 19.3 d.f. = 1, p .001).

This observation is curious since Laws (1970) has calculated that the ‘musth’ gland of an adult bull weighs three times that of an adult cow, and it would therefore be expected to show a greater activity.

The secretion in some cases seems to be related to arousal and is probably stimulated by the autonomic nervous system. I made several observations of both cows and bulls that had dry temporal glands which began secreting during the course of an excited threat display. In one aggressive interaction between a young bull and a large cow both had wet cheeks at the start, but the secretion spread considerably in both animals over the course of ten minutes (see Fig. 6.3 p.,102). Dr. H. Croze (pers. comm.) observed the death of a cow in the middle of its family unit and describes how a few minutes after the cow had collapsed almost every member of the family begun to show strong temporal secretions, as they attempted to raise her, although their cheeks had previously been dry.

It is difficult to relate the secretion to any specific behaviour pattern beyond general excitement, and I have even observed several highly excited bulls and cows that showed no secretion. The chemical composition might be important and could possibly be varied in different contexts. Usually however if one member of a group has a strong flow the other members were likely to show the same. In some individuals the gland on one side of the head was seen to be active while the other side was dry. I have observed the flow varying in one individual from day to day, but once again without any direct relationship to obvious changes in behaviour.

The frequency of secretion among adults may be related to density. In Serengeti the secretion ratio was less than 10 per cent in adults (Croze, pers. corn.), and in the Tarangire National Park, between June and August 1969, it was 25 per cent (n = 48, pers. obs.) compared to a secretion ratio of 54 per cent for bulls and 90 per cent for cows in Manyara (see above Table 6.1). Whatever social signal function the secretion may have, the frequency of transmission is likely to be related to the frequency of inter-individual or inter-group contacts. The Manyara population has a very high density, of more than 5 elephants / km^2 (Chapter 4) compared to the Serengeti with less than 1 elephant / km^2 Dr. H. Croze (pers. comm.) and the Tarangire with a mean yearly density that ranged between 2.5 and 1.16 elephants/ km^2 (Lamprey 1964). The Tarangire density may have increased since Lamprey's study due to a decrease in the elephant population's range, but from casual observations of elephant groups during 22 radio-tracking flights in that area between May and July 1969, I formed the impression that the elephant density was very much lower than at Manyara. The number of inter-group contacts would be expected to be higher at Manyara than in the other two areas, and this may explain the higher percentage of elephants with temporal secretions. A comparative survey of temporal secretion rates, particularly in areas where large elephant concentrations tend to build up seasonally such as the Serengeti (Hendrichs, 1971). And where the intergroup contact rates must also increase, would be of great interest in establishing whether or not there is a relationship between the temporal secretion ratio and frequency of social contact.

A number of functions have been suggested for the musth glad, Sikes (1971) suggests that elephants are territorial animals and that the approach of strange animals may set off a train of aggressive behaviour including hasty scent marking with the temporal gland which is rubbed against tress. Since her observations were not based on known animals and hence she would not be able to know the home range of a resident animal in order to distinguish it form a stranger, her interpretation of intraspecific aggressive behaviour as territoriality must be regarded with some caution. I have been unable to confirm her observation that the approach of one elephant, strange or otherwise, elicits cheek rubbing in another. Laws (1970) has suggested that the temporal gland might function as a trial or home range marker. Kühme (1963) mentions that a male zoo elephant frequently touched its temporal gland as if to seek reassurance during approach–withdrawal conflicts. Some functions suggest themselves from studies of other species. Ralls (1971) has reviewed mammalian scent marking and stresses that mammals mark not only when they possess a territory but also when dominant to or intolerant of others Mice (Muller–Velten, 1966) and mongoose (Rasa in press) use scents as alarm signals. One scent may also serve several signals.

As African elephants do not appear to be territorial animals (chapter 5), the present evidence suggests that trail or home range marking, individual recognition and perhaps alarm are the most likely functions of the 'musth' gland. The higher frequency of female secretion at Manyara might then be related to the greater need for cows and calves to keep contact, particularly in the confusion of elephant scents present in large aggregations. Certainly the 'musth' gland of' the African elephant behaves very differently from that of the Asiatic elephant where it probably serves a different function. (Short, 1967; Eisenberg et. al. 1971; Jainudeen et. al. 1972). For instance musth in Indian elephants is found mainly in bulls and not before the age of puberty. It occurs periodically, and is associated with aggressive behaviour and with an unusually high testosterone level in the blood, but is not obviously correlated with sexual activity.

Both faeces and urine sampling may have a communication function. When a bull encounters a cow he often extends his trunk to her genital area smelling or touching her, and then almost invariably putting his trunk tip into his mouth, probably touching the large and well developed Jacobsen's organ, which opens into the buccal cavity (Eales, 1962) Fig. 6.5. This sensory organ in other mammals is used in almost exclusively sexual contexts (Knappe, 1964), and sniffing behaviour at oestrous by bulls almost certainly serves to detect the sexual condition of partners, comparable to 'flehmen' in other ungulates (Knappe, 1964).

Sniffing may also be performed by juvenile animal and by very young calves. Faeces may even be picked up and placed in the mouth. Faeces and urine sniffing in non-oestrous conditions may have any of the potentiaI functions described for the 'musth' gland.

A third form of trunk contact is seen when young calves place their trunks in the mouth of the mother during feeding (Fig. 6.6 A, B). This is usually followed by feeding and it seems that the calf is sampling the food which the mother is

Figure 6.5
Sexual sampling.

A. Adult bull and young oestrous female.

B. Bull explores female genitals with trunk.

C. Bull sucks tip of trunk after sampling.

D. Bull in excited state before copulation.

eating. Sometimes the calf will pull some of the food out of the mother's mouth, and after chewing, swallow it.

Among animals of all ages and both sexes the insertion of the trunk into another's mouth almost invariably occurs when two individuals meet. (Fig. 6.6 C, D). The smaller animal is usually the first to insert its trunk and it is possible that this behaviour originated as food sampling in the calf and has developed into a form of appeasement signal used when an inferior animal approaches a superior. During play fighting it is common to see the trunk inserted into the rival's mouth, possibly serving to keep the level of aggression under control; Perhaps, however, both adults and calves gain information on where the other has been and what food it has been eating.

The meeting gesture may also appear without physical contact when the trunk is pointed or moved in the direction of an approaching individual. The accentuation of this movement suggests that it is a social signal which may have become ritualized from what it was originally a sensory olfactory movement or a food sampling intention movement.

Touch

Observations of Asiatic elephants show that they are highly sensitive to touch in any part of their bodies. (Deraniyagala, 1955). It is therefore likely that African elephants are too. In many of their interaction elephants touch each other with their trunks or lean and rub their bodies together. In the subsequent sections I shall describe in core detail the interactions observed in particular situations.

Interactions within the family Unit - Parturition

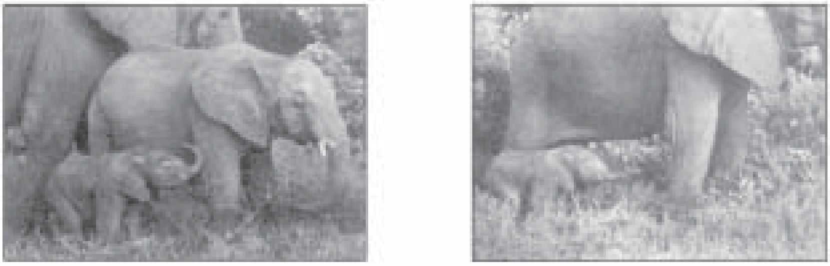
Parturition in the wild has been described by Poppleton (1957), Young (in Sikes, 1971), and Nutter (1971); and in greater detail in captivity by Lang (1967). I have never witnessed the actual moment of birth, but three times I have watched calves that had certainly been born on the same day. As such accounts are very rare I describe these observations in detail.

> On a morning in August 1967, I encountered DEI F.U. in a clearing in the South Endabash scrub. A young female of 14 years had just given birth. Under her belly stood a very small calf which was still covered in wet blood. Blood also covered her hind legs and trunk, and it was smeared on the trunks of two large females of this group, suggesting that they may have picked up the afterbirth, as reported by Poppleton (1957). All the elephants were standing doing little, until they became disturbed by my presence. They trumpeted and shook their heads in threat but remained at 50 metres neither attempting to charge nor run away. I left in order to spare them further disturbance.
>
> At dusk on a day in March 1968, I located LEO F.U. emerging from the Musasa River and walking towards

Figure 6.7
Slender Tusks and her newborn calf less than 12 hrs old.

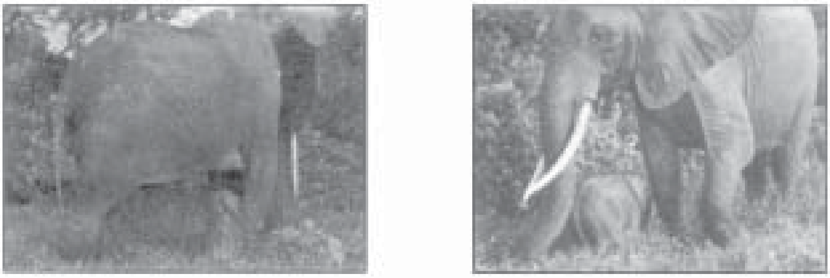
A. Slender Tusks and a newborn calf.

B. Mother supports calf with foot and trunk.



C. Calf attempts to suck from sibling.

D. Calf explores with trunk extended.



E. Calf collapses after sucking.

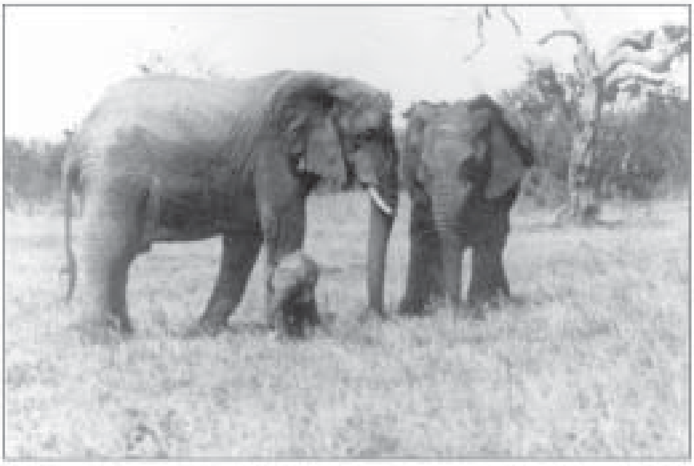
F. Mother turns around and pulls in calf.

G. Relative sizes of Slender Tusks, newborn calf and $4^1/_2$ year old sibling.

Photographs by courtesy of Mr. L. Nutter.

Figure 6.8
The birth of a calf.

A. **Bull lays head on mother.**



B. **Bull and mother smelling afterbirth.**

C. **Other F.U. members join mother and calf and smell afterbirth.**

Photographs by courtesy of Mr. L. Nutter.

Acacia tortilis woodland. I had previously seen this group on the morning of the day before and had checked out every member. The second largest female, slender Tusks, was now seen with a new-born male calf. As no blood was visible on the calf or the mother it must have been born before the shower of rain seven hours previously. The following sequence is illustrated in Fig . 6.7 A - G from field notes:

"The calf is very unsteady on its feet. Its legs are weak and its feet seem to hurt it as it walks. The head has an elongated squashed look (characteristic of young elephants). Its eyes are half shut and it moves its trunk up and down, evidently exploring for a place to suck. It makes hesitant attempt to suck, but falls down frequently. Each time the mother helps it up onto its feet using her forefoot and trunk (Fig. 6.7 B). The calf now walks up to its elder sister of 41/2 years. She is well aware of it and turns her head slightly towards it extending her trunk (Fig. 6.7 C). Slender Tusk's breasts do not look very big. She pays little attention to the calf and is grazing vigorously. (Fig. 6.7 D). It walks after her stretching its trunk out. The calf collapses, she turns round and pulls it towards her and nudges it upright (Fig. 6.7 F). The calf stands still for 10 minutes swaying, with its eyes closed."

At this moment the family unit was widely dispersed. Leonora, the matriarch, was 100 metres ahead with her two calves and two other young cows with their calves were 50 metres ahead. Slender Tusks was only accompanied by her own female calf, which paid great attention to the new-born. The mother's behaviour appeared to be quite unaffected by our presence and she walked past the landrover with her two calves at 10 metres' distance.

The notes continue :

"The calf falls down again and is nudged up with a foot. It falls immediately again and is lifted by the mother's trunk. It raises its trunk to her breast. The mother walks on a little, but the calf cannot keep up. She turns around and stretches her trunk towards it and waits. It catches up. Slender Tusks growls and Leonora, the matriarch, and the others answer from 100 metres away. The calf raises its head and sucks for 15 seconds, pauses with head down for 20 seconds, then up again for 40 seconds, until the mother then pulls away. It can only reach the teat with a great effort. The older calf, which has wandered off, returns and tries to suck, but slender Tusks growls at it and Pushes it away with her forefoot. A giraffe passes by within 40 metres. Slender Tusks shakes her head at it. At 19.15 hours it becomes too dark to see."

The behaviour described covered a period of 25 minutes.

The next day l located the same family at 7.30 a.m. They had moved almost exactly one Kilometre in the night. I watched them for 15 minutes in dense vegetation before they became disturbed, during which time

I was able to measure the shoulder heights by the pole method (Ch. 4). Slender Tusks had a height of 245 cms., the elder sibling 160 cms and the new-born 85 cms., equivalent to ages of 30 41/2, and 0 years respectively. The new-born was still unsteady but noticeably firmer on its feet. It fell down twice in this time near to its mother and was helped up once, but recovered by itself the second time.

On the third occasion in July 1969, l watched APH F.U. with a new-born calf for more than one hour in the middle of the day, on the edge of a road leading up the escarpment. There were 9 members of this family, and 6 of these were in a tight cluster, each almost touching the next, within 13 metres of the road. Tusked Ear, a cow of' about 15 years, had just given birth to her first calf, a male which stood shakily by her side. The afterbirth lay in the road, but it looked as if all the animals except for the new-born had touched it, as their trunks were bloody. One of the females present was a fully grown cow, Electra, with two calves of her own, one of 5 1\2 years, and another just under a year old. The remaining individual was a female of about 9 years old. The new-born explored with its trunk making several, only partially successful, attempts to suck from its mother. She looked very tired and stood with her head drooping, paying no attention to the calf. After 10 minutes the calf approached the large female, Electra, and walked under her stomach. Electra promptly kicked it with her hind leg three times, sending it sprawling. The new-born staggered to its feet, wandered back towards its mother and was protectively straddled by the 9 year old female. The mother extended her trunk and touched the baby, where it stood under the 9 year old. Eight minutes later the calf once again approached the large female, Electra. Once more it was kicked away roughly, although Electra did touch it gently with her trunk. It approached again two minutes later and was once more kicked away. It now collapsed on its sternum and enrolled on its side. The 9 year old straddled it again and rubbed its back with her trunk. It rolled onto its front. All this occurred while the others stood peacefully in the same spot browsing, despite the passing of several cars within less than 15 metres; **Tusked Ear**, the mother, kicked up dust distractedly. A noisy lorry rattled by and the 9 year old pushed the new-born to its feet with a forefoot. It staggered back to its, mother and attempted to suck unsuccessfully. At the same time the large female Electra, allowed her younger calf to suck. The new-born turned to the nine year old and tried to suck from her. Electra then wandered off with her own 2 calves. The 9 year old began to follow her, but then turned back and put her trunk out to the new-born, as if soliciting it to follow. Tusked Ear growled gently and Electra cameback. The new-born managed to follow the 9 year old for 5 metres before collapsing again. This slow progress continued, with the mother and the 9 year old standing for long periods with the new-born in between them, until finally they disappeared from view down the steep, rocky hillside.

These observations illustrates some interesting behavioural points. There was no indication on that the event of parturition in any way affected the normal spacing of these family units. The pregnant cows did not leave their group but remained integrated nor did the groups concentrate around the pregnant cows any more than they might normally do. Family members in each example were within earshot of each other, remaining in vocal communication and could have concentrated rapidly if help or defence of the new-born against predators were needed. Apart from the 2 young females which showed particular interest in the babies (see also Young, 1971, and Lang , 1967) , family unit members showed no great excitement over the births , and their attitude towards vehicles was no more aggressive than usual. In contrast Poppleton (1957) recorded that all members of a large group showed great interest in a birth and bunched around the mother. Nutter (1972) observed that a mature bull came to investigate a new-born calf, and laid his head on the female's back, and later other cows and calves crowded around her (Fig. 6.8 A - C).

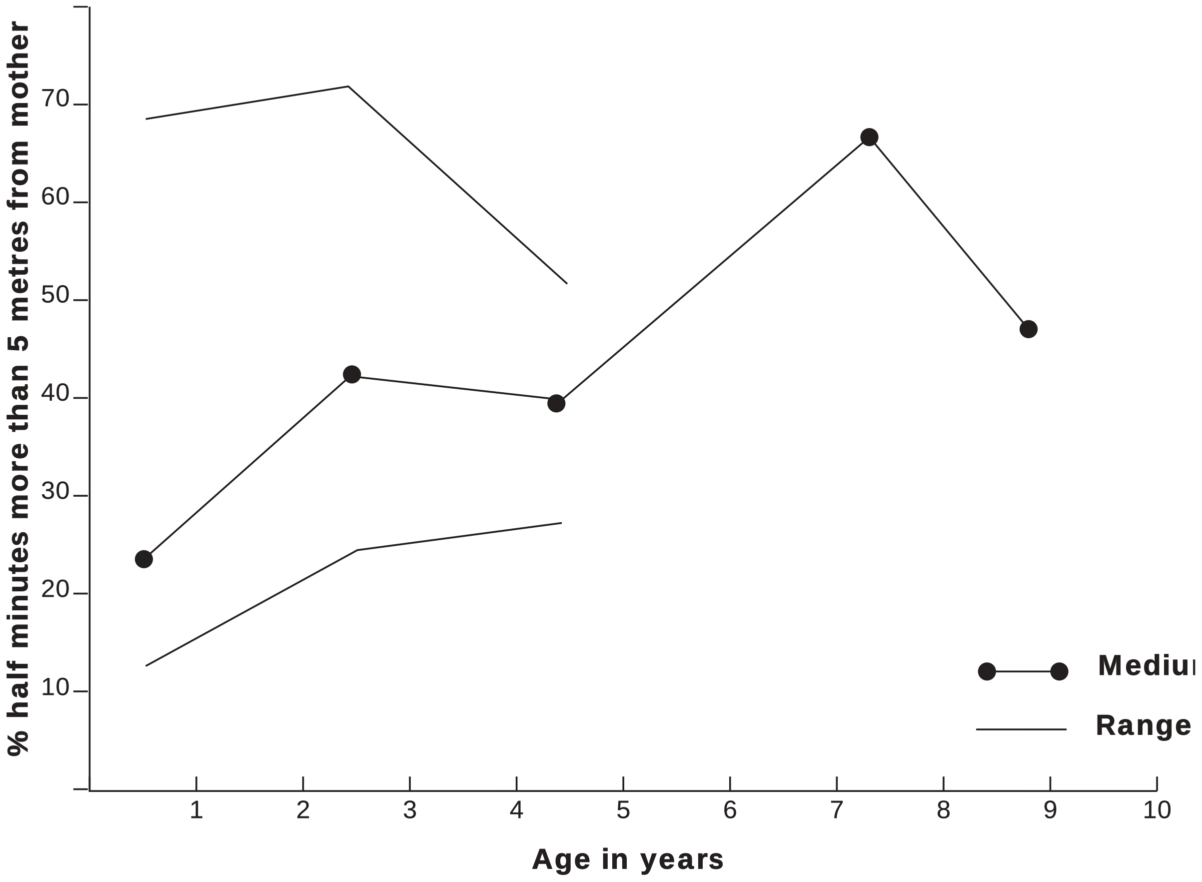
The rejection of Tusked Ear's new-born by Electra is unusual and a typical. Cows will usually suckle any other small calf, and Electra demonstrated how variable behaviour can be in an animal as complex as an elephant. This observation demonstrates that a calf may be the recipient of social aggression on the first day of its life. All even more extreme example was recorded in the Mikumi National Park, Tanzania, when a cow picked up its two month old calf and then trampled it to death (Mr. S. Stephenson, 1969, pers. comm.) for no apparent reason.

The Cow Calf Bond

In its first few weeks a baby elephant is still shaky on its legs, and receives constant help from the mother or often from a teenage female. In fact, all through the first year the mother is keenly aware of the movements of her offspring. Any attempt by the baby to run further than 15 to *20* metres away, usually causes her to go and retrieve it. Much of the time they are in actual physical contact, spending long periods with the calf leaning on the mother. There are few minutes that pass without some, form of tactile contact, whether it is the rubbing of flanks, a touch of the trunk, or a bout of suckling. As the calf grows its relationship with its mother changes. Gradually it spends less time by her side and more time with other calves.

In addition to everyday observations, l was able during two periods in August 1968 and August 1970, to quantify the development of the cow/calf bond by recording mother/calf interactions, involving calves of different ages. For this l used check sheets divided into half minute intervals. On Professor Hinde's advice, the methods of recording and analysis were modelled on Hinde and Spencer-Booth's (1968) study of mother/infant interaction in rhesus monkeys, although the field conditions were

Figure 6.9
Calves' time spent > 5 metres from mothers



Although calves show greater independence from mother with age, even at nine years old, a calf may spend 45% of its time less than 5 metres from its mother.

naturally less controlled. The chief measures were as follows:

1. Percentage of half a minute that the calf was more than five metres from its mother, out of the total number of half a minutes in which it was recorded.

2. Percentage Approaches by calf minus Percentage Leavings by calf (% AP^c - % L^c): Every time that the distance between the mother and calf increased from less than 5 metres to more (Leavings), and vice versa (Approaches), l recorded whether the change was due to movement of the mother or the calf. The difference between the percentage of approaches and the percentage of leavings due to the calf gives an indication of whether it is the mother or the calf, which is mainly responsible for maintaining proximity. When the mother tends to do more approaching than the calf the value will be negative.

In all, 17 calves were observed for 100 to 150 minutes each, mainly in the mornings and evenings, when the elephants were active. The ratio of time spent recording, to time, spent in (my) manoeuvering for position was 1 : 10. The calves' ages were distributed as follows:

6 in the 0 - l year age class
7 in the 2 - 3 years " "
2 in the 4 - 5 years " "
1 of 7 $^1/_2$ years
1 of 9 years

Three of the O - 1 year olds, and one of the 2 - 3 year olds in 1968 were observed again in 1970 when they were two years older. Only uninterrupted observations of undisturbed elephants that lasted for atleast 15 minutes have been analysed. The results are summarized in Figs .6.9 and 6.10 and show the median values for all calves and the range in behaviour between individuals.

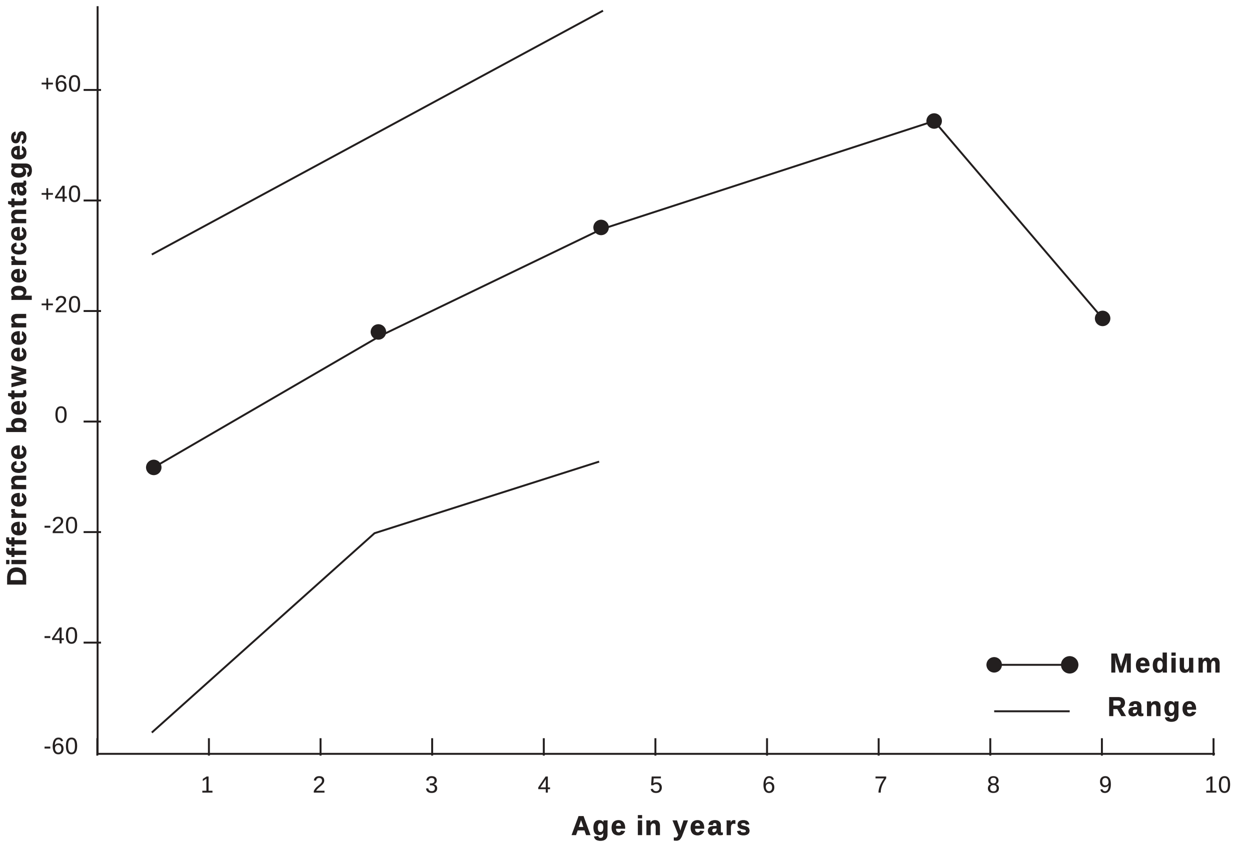
Proximity to Mothers. (Fig. 6,9)

As the calves grew older they spent more time further than 5 metres from their mothers. The differences between individuals were marked: some calves were very independent from their first few weeks setting out apparently intrepidly to explore their environment. One exceptional calf spent more time in its first year with the pregnant matriarch than with her mother. It is nevertheless remarkable that even after 9 years, a calf may spend up to 55 percent of its time less than 5 metres from its mother. In Chapter 5 (Fig. 5.5) it was shown that even after she became pregnant, Mkali, a 13 year old female continued to stand nearest to her mother, rather than any other adult in VIC F.U. These consistent spatial preferences of a young animal confirm that the cow/ calf bond may persist into adulthood.

% Ap^c - % L^c. (Figure 6.10)

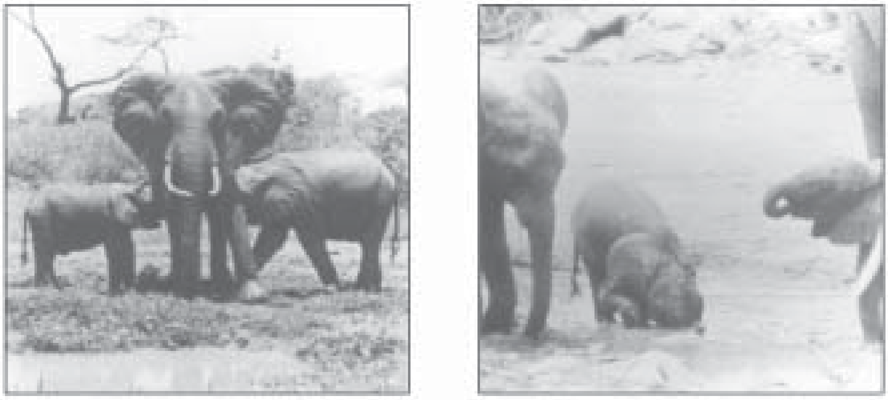
In the early stages, a calf receives a great deal of attention and this is reflected in a negative % Ap^c - % L^c value. Small calves in the first 6 months often get stuck in mud

Figure 6.10
% approaches - % leavings for calves (see text)



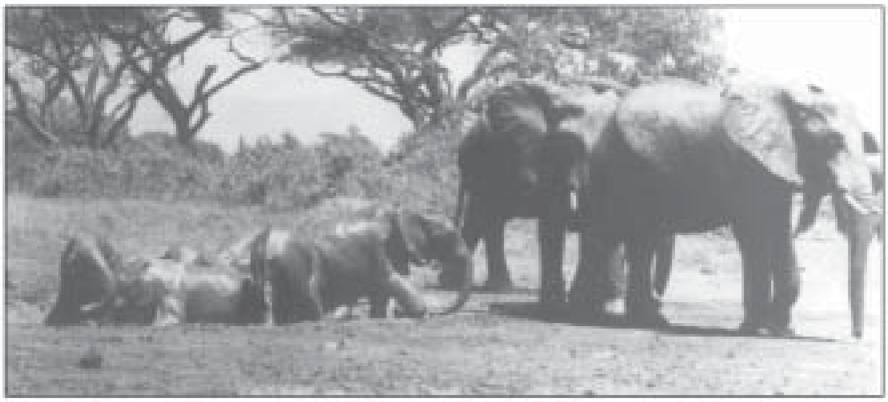
When the value changes from negative to positive, it shows that the calf follows the mother more frequently than vice versa.

Figure 6.12
Calf behaviour

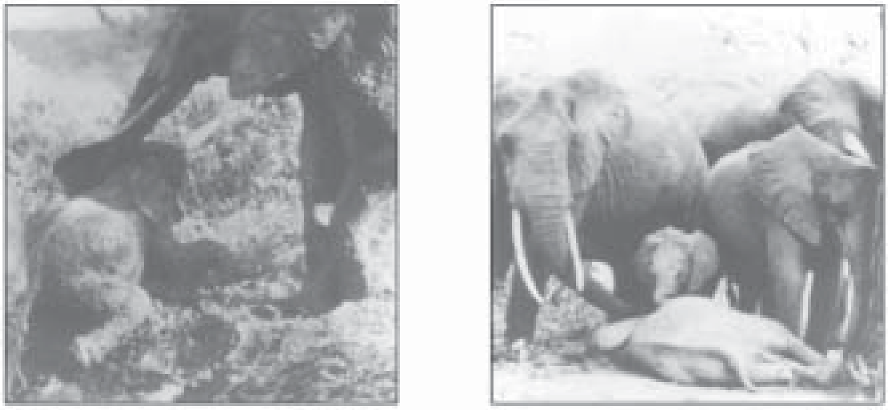


A. Simultaneous suckling of siblings.

B. Drinking by mouth before learning to drink with trunk.



C. Play group of juveniles in the wallow.



D. Mother pulls calf out of wallow.

E. Juvenile calf asleep in family unit.

wallows or have difficulty in surmounting a wallow's edge or fallen log. Often the mother may help the baby negotiate the obstacle by lifting or pushing it with tusk, trunk or forefoot. (Fig. 6.12 D). When wallowing both the mother and other individuals appear very careful not to tread on small babies.

From 6 months on, the calf wanders at ever further distances. In part this seems to be due to an increasing indepedence on the part of the calf, but seems to be caused largely by the mother's growing indifference to moment to moment activities of her calf. From intensive mothering the relationship changes into a leadership-followership, where the calf has to keep up or get left behind. Consequently, % Ap - % L changes *from* negative to positive.

On average when the calf reaches approximately 4$^1/_2$ years of age a younger sibling is born. (Chapter 8). From now on the older calf takes second place at its mother's side, and spends more time near to other calves. Some calves may stand closest to calves of other mother - offspring units more often than to their own mother's or younger siblings. (Appendix, 3.7)

Help for a calf in difficulties is still forthcoming. In fact, this is not confined to calves but develops into a system of mutual aid and concerted group defence which benefits all members of elephant society.

Suckling

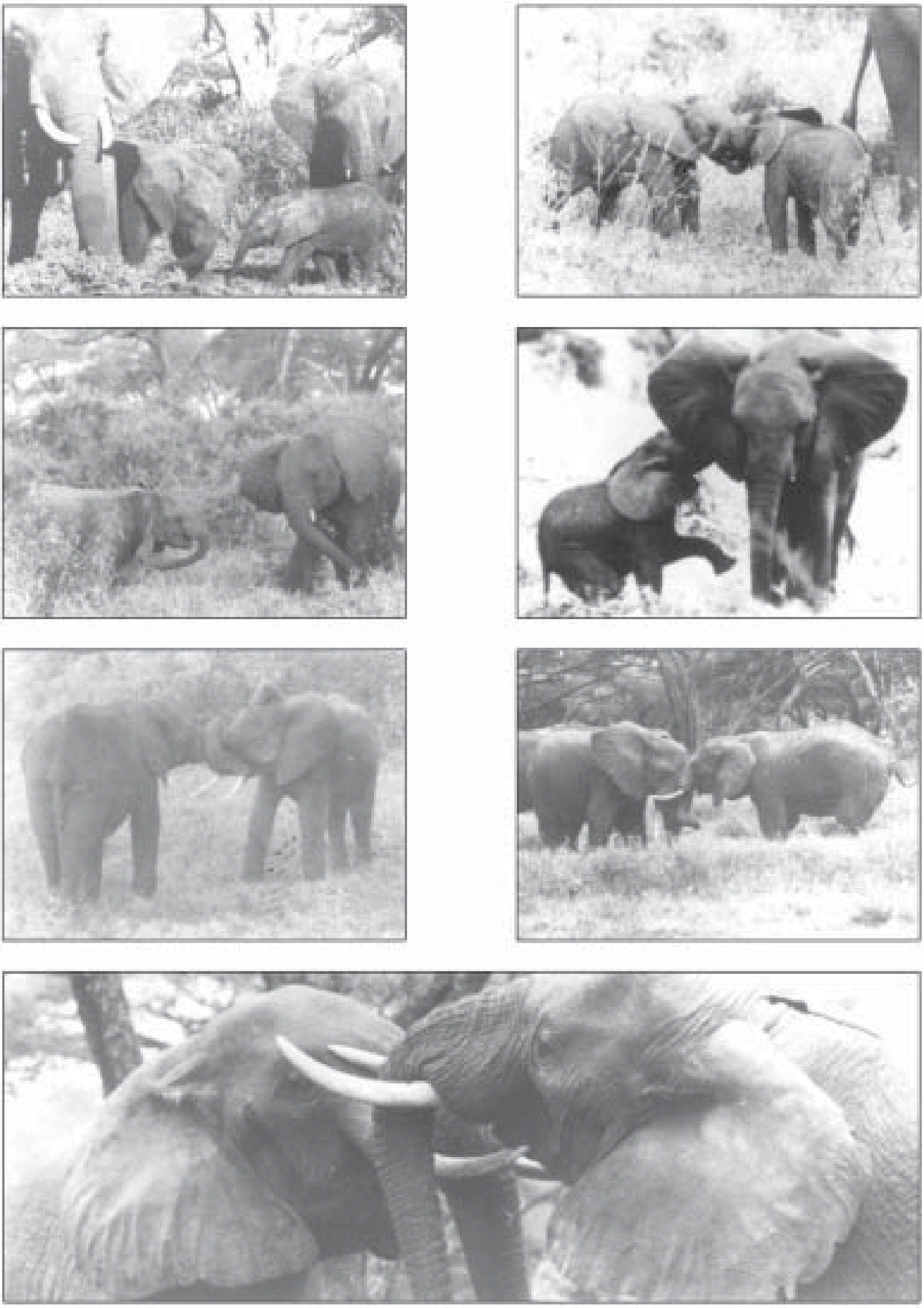
Slender Tusks' calf initially made sucking attempts at a variety of places on the mother's and older sibling's body, in particular pushing up between the front and hind legs. Within the first three days it learned to suck between its mother's front legs, after which it made no more false attempts. I was unable to measure the frequency of suckling as although mother/calf separations could be quantified, the calf was often out of sight and may have been suckled by another female. Even when they were together their finer activities were often obscured.

Calves on average sucked in bouts of 30 seconds (range 1 - 75 seconds). One female might suckle sibling calves of different ages simultaneously (Fig. 6.12A) and many females suckled calves of the F.U. other than their own (like elephant seals, Le Boeuf, 1971). Rejections of calves from the nipple increased with the calf's age. A female may pull away, block the calf with her forelegs or push it away with her trunk or tusks. Calves continue to suck for as long as they are tolerated and may still be suckled at 7 - 8 years of age. As their tusk; grow the calves' frequent thrusting at their mothers' breasts appears to cause discomfort to the cows, and probably contribute s to the number of rejections.

Play Fighting

It is common to see aggression within the family units, both in the form of 'p1ay' fighting, and in competitive situations

Figure 6.13
Development of play fighting



when a slight threat gesture from the dominant animal is usually sufficient to resolve a conflict. The term ‘play’ is used because usually the fighting was performed at a low intensity and the partners seldom harmed each other. Elements of other behaviour patterns, such as short bouts of incipient mounting, appeared irrelevant. The ‘play’ partners usually refrained from pressing home an attack and the movements were less rapid than in all-out fighting often resembling the rough-and-tumble play of other young mammals, like puppies or primates. Nonetheless there was no sharp distinction between serious fighting and play. Even play fights sometimes developed into serious encounters in which the participants drew blood with their tusks particularly around the upper part of the trunk and gums of the tusks.

I saw play fighting even in calves that were under one month old. It was a frequent activity of all calves and immature animals. Calves less than one year old were often aggressive and rammed their peers, elder siblings, or mothers with the base of the trunk, where the tusks later grew (Fig. 6.13 A - D). The attacked animal usually responded in what appeared to be playful aggression and a tussle often ensued. In calves under 3 years of age play fights seldom developed into serious aggression. The partners were often of very unequal sizes, a 6 month calf might attack a 13 year old but the encounters were characterised by great gentleness on the part of the larger animal. Calves from 3 to 9 years old sometimes knocked over a first year calf apparently by mistake, through playing a little too roughly. This almost invariably provoked an immediate response from the mother who joined in her offspring’s side, jabbing at the older calf with her tusks or knocking it with her trunk. Behavioural differences emerged between the sexes around puberty. As the young females became increasingly maternal, they appeared disinterested in fighting, while in contrast young males tussled with greater vigour than before. Above the age of 10, it was not unusual to see semi-serious fights between young males. Bulls may continue play fight well into maturity but mature cows seldom do so. In Fig. 6.14 a play fight between two adult bulls may be contrasted with serious fights between younger bulls in Fig. 6.15 A’– C.

The elements of play fighting in the wild are in most respects similar to Kühme’s (1962) description for three captive animals, although wild animals exercise a wider choice of partners. Play fighting was more frequent in the evenings. It might begin at a distance by one elephant using any one of the threat displays described on page 103. Among these was the upward head jerk described by Kühme (1962). Frequently it began when one animal simply rammed another in its side. When play partners advanced, their heads were raised and they pushed each other at the base of their tusks with trunks entwined. The heads were then twisted while each tried to force the other at a disadvantageous position. If the animals had tusks, they would try to use them as levers, each trying to force the other’s head down or sideways (Fig. 6.13 E’– G). The trunks grappled and often the tip was placed in the opponent’s mouth. If the animals broke apart, the one that turned away might be prodded gently in the flank by the victor. When separated they often stood apart with their tusks in various attitudes. Kühme (1961) has stated that curving the trunk backwards over the head " is without doubt an action expressing conflict between attack and flight tendencies which is understood by the partners", and that "probably bulls living in the wild threaten each other in this way before the fight". However this posture is one often seen in the wild, not in aggression, (Fig. 6.3 F, pg. 102), but also when animals are testing their air for scent. The sensory movements may be just as accentuated as the aggressive ones and in this context, the trunk's signal function remains to be proved. Bull threats that I observed were usually made with the head and ears and not with the trunk (Fig. 6.20 A).

Like Kühme's animals, elephants at Manyara were adept in using ground to their advantage. At times play fights would resume with redoubled fury when the two opponents found themselves fighting across a fallen tree, which effectively acted as a barrier to movement.

Play fighting may as well teach an elephant to avoid fighting a stronger animal and may provide a mechanism to make frequent tests of its position in the hierarchy without being hurt. The experience gained might also be useful in more serious fights.

In competitive situations over food or water holes threat displays were used, but serious fighting occurred extremely rarely. Threat in elephants, as in so many other species (Tinbergen, 1951), appears to protect an individual from actually being attacked.

Behaviour at puberty

As the calves approach puberty, marked behavioural changes take place. A young female from about the age of 9 years tends to remain strongly attached to her mother but begins to pay great attention to her own younger siblings and to the small calves of other cows. She tends to spend more time than the mother in playing with the calves. When moving in a group, she keeps close to the calf. When stationary, she frequently touches it, straddling it with her forelegs and pushing it under her belly. In one example a family was alarmed by a passing vehicle and a 3 month calf ran in panic away from the group. A teenage female headed it off and used her trunk to push it back towards the family. Another time a calf fell asleep and remained lying down as the group moved off. Again, it was the teenage female who remained with the calf and awakened it with a push of her forefoot.

Once I released a 9 months old calf, which I had found isolated in the proximity of a strange family unit. It ran to join the family unit and for two days remained with them. I saw the mature females suckle their own calves but the strange one. Only a 12 year old female paid it attention. However the calf gradually lost strength and eventually collapsed. The young female attempted to lift it while the others moved on. When this failed she walked away 100 metres with the group and then rushed back to the calf, excited and trumpeting. She stayed a few more minutes before reluctantly abandoning it.

In some family units older females seemed to resent the attention paid to their own calves by the immature female offspring of another cow and on several occasions, I saw an older female chase away a younger female that had been persistently following and touching the older one's infant calf.

Similar maternal behaviour has been observed in the immature females, Eleanor, a tame animal in the Tsavo National Park (Sheldrick, 1972), which in the recent drought (1971 – 72) adopted a number of abandoned calves, brought in by the National Park Rangers. Adoption and suckling of a strange calf has also been recorded by Woodridge & Trevor (1970) in the wild.

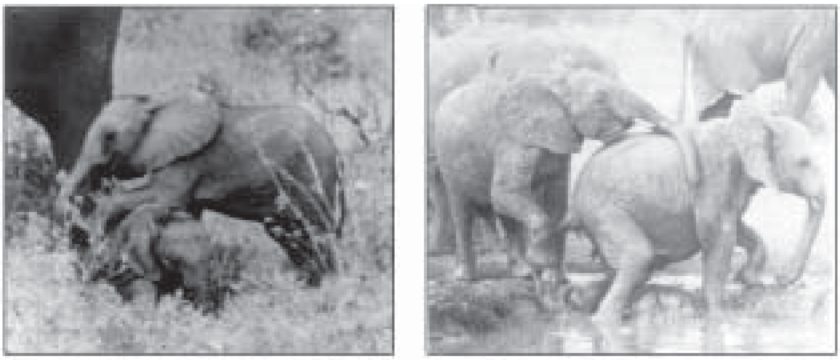
This 'aunty' behaviour of immature females may be functional both in increasing the survival chances of closely related calves in providing the young females themselves with experiences which may help them later in raising their own calves. On average females gave birth to their first calves at the age of 13, when they were still far from fully grown. Younger mother s tended to be more maternal than older mothers .

Young bulls develop very differently. From an early age their play fighting is much rougher. Sexual behaviour appears in the first year (Fig. 6.16 A - C) and in the middle of play fighting a young bull may mount its partner, behaviour never seen in female calves. As they grow up, their sexual behaviour and fighting appear to irritate the adult females, including the young male 's own mother. At first the cows may only shake their heads or flap their ears at him. But later, from approximately the age of 11 years, it is common to see larger cows make completely unprovoked attacks on young bulls even causing open wounds by jabbing then in the flank. At this age the young males begin to keep out of the way of the cows. The attraction for the family unit still persists. If alarmed, a young bull will run back to his family. He also often play fights with other juveniles, when he can do so without being attacked, but a close approach to a large female sooner or later provokes attack (Fig. 6.16 D). At the same time the young male meets and plays with many already independent bulls, and spends prolonged periods in their company, or follows the family at a distance.

I recorded the disappearance of 15 young bulls from their families. Some of these animals may have died, but two l saw very frequently throughout the study period.

> One, called Radio Robert, belonged to BOA .F.U. and was radio-tracked for four months from April to July 1969. His shoulder height measured directly during the immobilization operation was 257 cms. which corresponded to the age of 19 to 21 years (Laws 1966, Laws, et. al. 1970). He was the largest male still attached to a family unit being already larger than some of the mature females, and once I saw him chase some small cows and their calves away from a drinking pool,

Figure 6.16
Male calf development



A. Mounting in first year.

B. Incipient mounting.

C. Immature sex play in proximity to matriarch.

D. Young bull chased away from family by matriarch.

when he encountered them beyond the protection of the large matriarch From 1967 on, he seldom came near the centre of the family unit but consistently remained on the outside.

During the immobilization operation he had been attacked by several of the larger females, which ran at him and knocked him over as soon as he started swaying from the effects of the drug. When he was inert some of them tried to lift him while others continued to attack him.

After he had recovered, from April to August he kept well clear of the large females, although he was consistently found within a few hundred metres of BOA F.U. He finally left BOA. F.U. in August 1969 and explored areas in the South where l had never recorded his group before or since. I never saw him associated with them again.

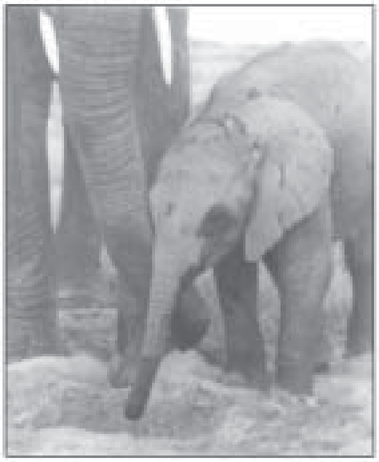
The other young male belonged to CAT F.U. Throughout 1966 and 1967, at the estimated age of 9 and 10 years, he appeared to be integrated and well tolerated. In 1968 l noticed a change. He spent more time at 50 to 100 metres from the nearest member of his family. At times be left them altogether and associated with HEL or JAG F.U's both of which belonged to the same kin group as CAT. On one occasion he approached too close and at 10 metres' range the matriarch turned slowly in his direction, which was enough to send him into rapid retreat, which incidentally shows how well he 'knew' that he was liable to be attacked. In early 1969 he began to associate for extended periods with mature bulls and was seen three times in February and March in their company more than 1Km. from CAT F.U. In April and May he was seen both with males and once for the last time with CAT F.U. Thereafter l never saw him associated with CAT F.U. again, and for nearly a year he disappeared from view. Then in June 1970 he reappeared and again one evening in August. I watched him engage in a serious fight with another slightly larger young male. (Fig. 6.15 C). CAT's young male appeared to be fighting much more vigorously and eventually chased the larger one away. Both young bulls were slightly gashed around the face. That evening CAT's young bull appeared to be in an aggressive mood. In the same evening he associated with BOA F.U. and threatened one of the large females, Giselle, by extending his ears forward. He did so from a position of safety on the edge of a bank so that she was at a disadvantage. Sequences of this interaction are shown in Fig. 6.3. At first the large cow and young bull fenced with their trunks, then they grappled and finally the movements became less tense and it looked as if the large cow had lost interest, being prevented from driving him away. Normally a young bull of that age would seldom approach such a large cow, let alone act so aggressively, and the incident suggested that he had deliberately chosen his ground.

The aggression of the cows towards young bulls seems to be the major factor in forcing them into independence Douglas-Hamilton, 1969). Whether such aggression increases with density has not been measured. Eisenberg et. al (1971) have recorded similar behaviour between cows and young bulls in wild Asiatic populations, and it is probable that such behaviour is a normal sequence in the life history of the bull. The wanderings of Radio Robert, and the disappearance of the other pubescent males suggest that it is usual for a young bull to extend or change his range when he becomes independent. The wandering from family to family within the kin group of the young bull of CAT F.U. just before complete independence, was also seen in three other young bulls at a similar stage. In VIC F.U. a young male of about 13 just before leaving tended to associate with the sub-group of the two young cows Guenevere and S.A.T., although they were both too small for either of them to have been his mother. Young females may also temporarily transfer from their own family to another within the kin group, but this usually lasts no more than a week and is relatively rare behaviour.

Cow/Calf Competition

This is seen most clearly at waterholes. Certain springs are highly favoured by elephants, probably for their mineral content. There may be space for only one elephant to drink at a time. Likewise in the dry season, when the rivers percolate beneath sand, elephants can only obtain water from a limited number of holes which they scoop out with their trunks. From these shallow pools individuals must suck up the water slowly if it is to avoid getting water in its trunk. The tolerance of a cow for her calf, and the hierachial position of each individual become clear at the waterhole. Calves try to push in when their mothers are drinking. The mother counters by pushing the calf away with her trunk, forefoot, or tusks (Fig. 6.17 A – F). Her action is usually accompanied by a deep growl. I once observed a 3 1/2 year calf pushed out of a hole 18 times in 5 minutes. The persistence of the calf usually means that as soon as the cow raises her head to pour water from her trunk down her throat the calf gains access to the hole and is able to sip some water before being pushed out again. Frequently in its clumpsy attempts to drink, the calf crumbles the fragile edge of the hole, causing its mother to move on or dig another. The tolerance of females varies greatly, but as in suckling, the younger the calf the more it is tolerated and a female's own calf is better treated than another's. I have sometimes seen older calves forcibly removed from a waterhole with a vigorous prod of the tusks. Calves over 5 years old usually do not attempt to push into a large female's water hole nor do they wait to get jabbed out, but there is much variation between individual mothers and calves. On several occasions l observed an older calf waiting for more than an hour before it could get a chance to drink. When the adults have finished they may walk away leaving the calves only a few minutes in which to gulp down, some water. It is not uncommon for another family unit, which has been waiting for the first to finish, to arrive and push away the waiting calves before they have had the chance to drink at all.

Figure 6.17
Competition within the family unit at the water hole.



A. Mother pushes calf with trunk.

B. Mother pushes calf with leg.

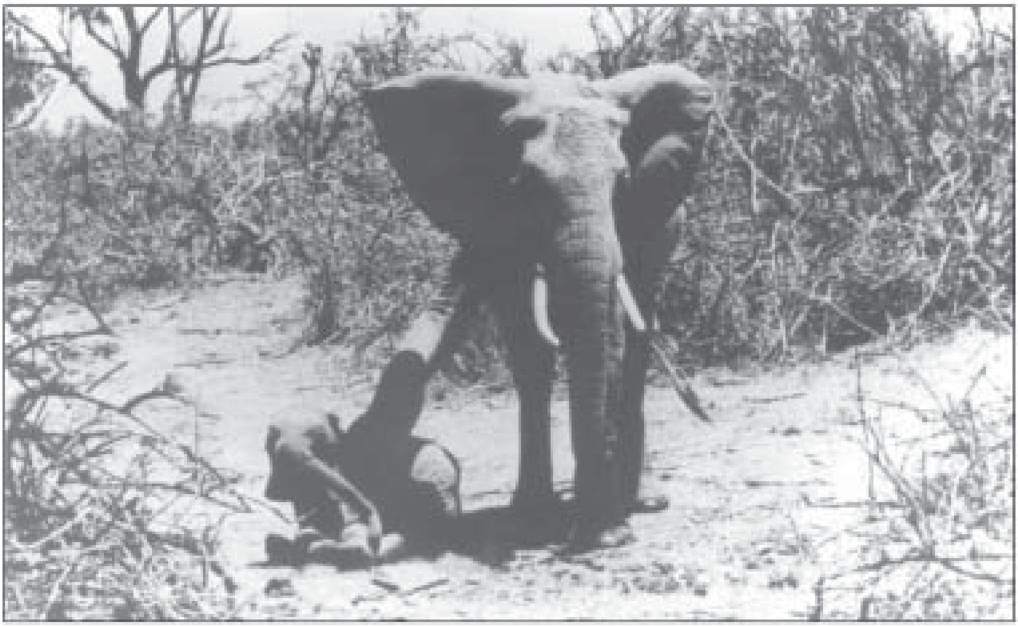
C. A tolerant mother.

D. Calf pushing in on mother.

C. Juveniles compete to drink after adults have finished.

Figure 6.18
Cow calf bond in stress.

A. A heat stressed calf stands by dead mother and sprays itself with regurgitated water.



B. A mother refuses to abandon her dying calf.

Photographs by courtesy of Simon Trevor

Thus we see that the mother/calf relationship is a complicated sum of interactions, developing with time in which a certain ambivalence exists between the actors with a great deal of individual variation. Mothers may momentarily reject their young as early as the third month, but in many cases a strong attachment lasts well into adolescence, which appears immediately in times of crisis. In the case of female calves the mother/calf relationship may develop into a permanent adult bond. Yet the mothers role in facilitating the independence of the calf must not be under-estimated. In the early stages conflict between the mother and calf arises when the infant attempts to run off to explore and play with other calves. Later however, the mother and calf may compete for food and water. In addition, the mother controls weaning, by avoiding the calf or thwarting it in its attempts to gain the nipple.

Under the Manyara conditions of plentiful resources, mother/calf competition never seemed to be intense, nor did the calves seem to be suffering from any deprivation. However, it is possible that would the necessary resources diminish, mother/calf competition might increase so that this form of social interaction could conceivably result in a higher calf mortality. This form of social stress' would be related only indirectly to elephant density insofar as resource availability itself was density dependent. Evidence from the drought in Tsavo suggests that even under conditions of extreme starvation the bond between a mother and her small calf may remain very strong. Emaciated females were seen attempting to save their dying calves and calves were seen which refused to abandon their dead mothers (Fig. 6.18, Mr. S. Trevor, pers. Comm.). Even whole family units would refuse to leave a fallen member and would waste time that could have been used searching for food (Sheldrick, 1972). Bonds between older animals appeared to weaken. Cows were unusually impatient with older calves and irritable with each other. Many cows and teenage calves were seen wandering alone and some of these deprived of the families protection were attacked and killed by lions (ibid.)

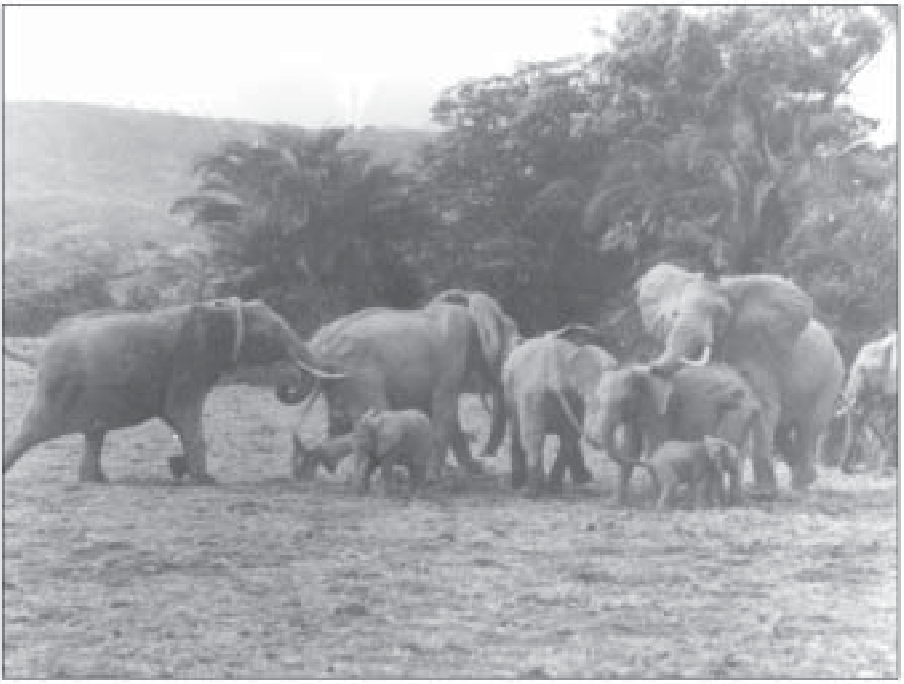
Cow/Cow interactions

Within the family unit relationships between females are usually tolerant. As described in the previous chapter, certain females form attachment to others but acts of aggression to other females are rare. In competitive situations the larger females usually predominates.

For example I once saw Victoria, the matriarch of VIC F.U., deprive SAT, a smaller cow, of a branch of *Acacia tortilis*, which SAT had just pulled off a tree. SAT waited until Victoria had eaten and departed and then went back to her branch, remaining behind and eating it while the rest of the family moved on.

In competitive situations of this sort, mild threat displays are used by the larger animals such as walking towards the other with head nodding or ears half extended, but attacks were rare, because the smaller

Figure 6.19
Inter-cow aggression



A. **Cow of JOC F.U. (on left) jabs cow of AET F.U.**

B. **Individuals of AET F.U. show alarm after attack.**

animal usually responded promptly by giving way. Likewise a hierarchy existed between family units, becoming evident at water holes.

On the occasions when one female did attack another, the reason was never obvious to me. The attacks appeared completely unprovoked. In Fig 6.19 A B a small female of JOC F.U. attacks a larger female of AET F.U. The attacks usually took the following form: one female suddenly rushed at another and jabbed it in the flunk with a tusk. The victim ran away and the aggressor usually returned to her group or continued feeding. I never saw a victim return aggression nor did I ever see a fight between cows.

Such attacks may be within the family unit, between family units of the same kin group, or between apparently unrelated groups. However, aggression never appeared even in the mildest form between certain females, such as Mary and Victoria or Guenevere and S.A.T. in VIC F.U.

These occasional jabs could potentially increase the probability of the recipient aborting if she were pregnant, but the infrequency of inter female aggression at Manyara makes it extremely unlikely that this form of behaviour had any significant effect on recruitment.

However, aggressive behaviour of other cows towards younger ones may be one of the main causes of the development of sub-groups.

Bull Interactions

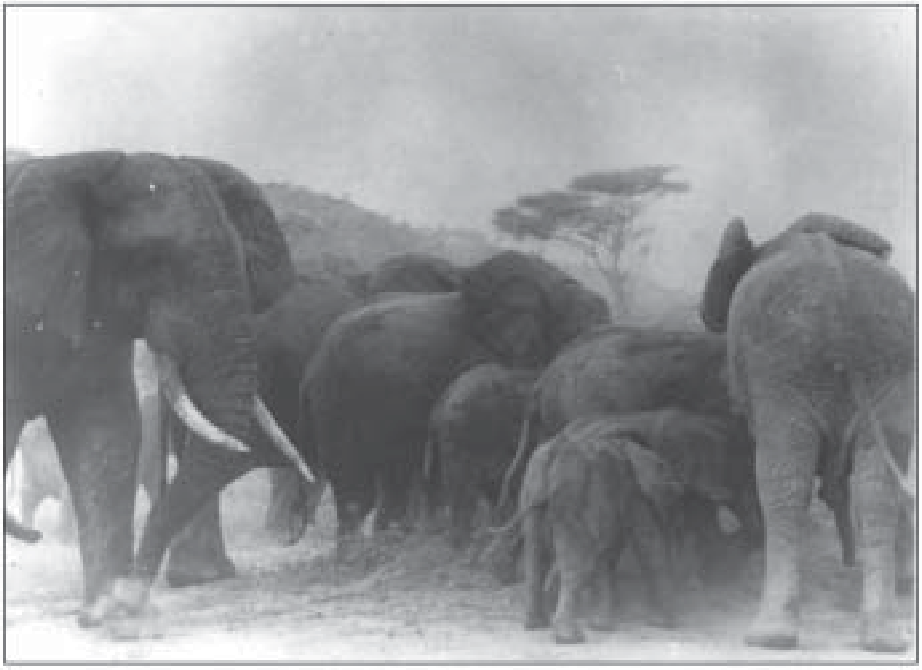
Serious fights between fully adult bulls were never observed directly, although one bull was found dead with what appeared to be a deep tusk wound penetrating his skull. Occasionally sounds of loud trumpeting and breaking branches came from the woodlands, and when I caught glimpes of excited bulls it appeared that a fight was in progress. As a rule, adult bulls appeared to have an understood hierarchy based on size and mild threat gestures, as in Fig. 6.20A where one bull standing over a waterhole threatens two others which approach, were usually enough to resolve any conflict. As with the cows there was nothing in their behaviour that suggested territoriality in the sense of a defended area. If their movements were affected by the presence or absence of other bulls then it was by attraction rather than avoidance. Tolerance between bulls declined only at times when a female came into oestrous, but even then smaller bulls moved rapidly out of the way when threatened by a larger bull.

Bull fights with a fatal outcome have occasionally been recorded in other areas (Wright, 1966; Bere 1966). Recently, following the 1971-72 drought, fighting was observed in Tsavo more frequently than before. During the mating season of 1972 Mr. S. Trevor found four dead bulls with deep tusk wounds in less than one month.

In their relations with cows and calves, mature bulls may sometimes be aggressive. A large bull approaching a

Figure 6.20
Aggressive behaviour of bulls

A. Centre bull threatens two approaching bulls who are also aggressively extending their ears.



B. Large bull (left) mildly aggressive with ear half extended approaches a family unit.

family unit may put his ears half forward in mild threat (Fig. 6.20 B), and at times the cows and calves run away. More often they turn to greet him by extending their trunks towards him or placing the trunk in his mouth, possibly in appeasement (p.112). One cow which was immobilised by a Ranger in the Addo National park, was actually killed by a bull (Anon., 1966, Afr. Wild. J. 20(3): 239) which tusked her head. It is possible that she failed to respond in an appropriately submissive manner under the effects of the drug. Woodford and Trevor (1970), also record an incident when an orphaned calf was released near a mixed herd. The calf ran up to a bull who knocked it over with his trunk. It then ran to a female who moved her forelegs to straddle the calf and allowed it to suck. Bull intolerance towards females and young is atypical however and their behaviour is usually gentle .

On many occasions I saw bulls approach a family unit and then smell the genital area of each cow, one after the other, as if sampling for sexual receptivity.

Sexual Interaction

Courtship and mating has been described for African elephants both in captivity (Kühme, 1962) and in the wild (Short, 1966; Buss & Smith 1966; Laws & Parker, 1968), and Short’s account covers three days of activity. In wild elephant courtship is reduced or absent. If a female is in oestrous she may be followed closely by up to 10 bulls but may still remain within her family. The bulls may show a copious secretion from their penis which l have seen lasting in some individuals for three to four days.

Elephants become excitable during the oestrous period. Trumpeting and growling are frequently heard, but observation is difficult. Although l saw apparently oestrous females followed by bulls on about ten occasions, l only witnessed copulation four times.

> The first time in May 1966, l was able to see little as the animals were obscured by thick vegetation. Among a group of elephants, a large bull mounted a small cow quite suddenly. His head and forequarters and the back of the cow were all visible above the top of the vegetation. A slight secretion oozed from his temporal gland and he remained up for about 45 seconds, while he and the rest of the group trumpeted and reared. Due to my inexperience, l did not dare to go closer than 230 metres to these excited animals and was therefore unable to make any further observations once the male had dismounted.
>
> In 1967 l observed a young male mount a young female for about 50 seconds. The female belonged to a group which at that moment was widely spread out. Both animals had slight temporal secretion and the young male appeared to achieve intromission. The mounting had been preceded by play fighting characteristic of immature animals, and it is possible that despite

intromission it was not a true copulation. A large number of males are usually attracted by females in oestrous, but in this case there was only the one.

The third copulation I observed occurred 15 miles north of the National Park boundary on the edge of the Kitete Chini swamp. In March 1970 I located a large breeding herd from the air and proceeded to follow them up on foot in order to find out if they were migrants from the resident Park population. In the afternoon I approached two large cow/calf groups of 30 and 25 animals. The cows were all completely strange to me and I believe that none of them had entered the Park during my study period. Within these groups were at least 5 large males including 2 that I knew very well from the Park. One of the Manyara bulls, who had just previously been wallowing, suddenly began to chase a young female which ran before him away from the group. He caught up with her after about 50 metres and while trumpeting, he softly pushed her hind quarters with his trunk. Then he laid his head upon her back and levered himself upright, with the help of his chin and trunk, until his forefeet were straddled on either side of her spine, with his trunk hanging straight down to the right side. Pelvic thrusts lasted for 30 seconds during which time he emitted deep growls. Before he dismounted, the rest of the group rushed up trumpeting. As soon as the female became disengaged, she was chased by another larger cow. The group milled around. Ten minutes after the mounting, two more large males joined this group. I lost sight of the original female but several elephants backed into others, trumpeting at intervals and the whole group moved off in a tight clump, with the males on the outer edges moving warily of one another.

On a fourth occasion l observed mating in semi-open Acacia tortilis woodland. In the morning of a sunny day in August 1970, I located VIC F.U. At the moment l arrived, one of the adult cows, named Innominate, burst out of a Capparis bush closely pursued by a large bull. She ran in a wide arc at top speed with the male rushing after her, his penis erect and flagellating. After covering about 200 metres at top speed, during which time l followed in the landrover, the bull caught up and reached for her rump with his trunk. She immediately stopped, evidently responding to the touch. He mounted and remained up for about 40 seconds. Both elephants were showing moderate temporaI secretions. Shortly after he dismounted, the rest of VIC F.U. arrived and rejoined Innominate, with much growling. All the elephants then calmed down and began to eat with the bull in their midst. No more sexual activity was observed throughout the day. The group moved into the shade of a dense clump of Acacia tortilis, and remained drowsily inactive or feeding until 15.30 hours. Four other family units FLO, LEO, OLD and SPH were sharing this patch of wood with them. During this time, a

> second bull approached Innominate twice, once at 13.55 hours and again at 14.30 hours. Although she appeared more aware of him than the other females were, she made no attempt to run away, neither did the second male make any attempt to court or copulate with her. All this time the first bull remained within 100 metres, apparently disinterested, making no attempt to rejoin Innominate. No antagonistic behaviour was seen between the two bulls.
>
> At 15.30 hours all 5 family units including VIC F.U with Innominate fully integrated, began moving out of the shade into an area of open grassland. The males made no attempt to follow and no more sexual activity or unusual behaviour was recorded up until dusk when observations were concluded.
>
> On the next day VIC F.U. was located from the air at 7.45 a.m. and ground contact was made at 10.15 a.m. The group was intermittently observed, when the visibility permitted, for two and half hours before contact was finally lost in very thick vegetation. Innominate was once more seen to be fully integrated within her family unit and no bulls were seen in association. It appeared that oestrous had ended.

There is nothing in these observations to support the contention of Sikes' (1971) that mating behaviour is affected by density. She suggested that herd dominance is disrupted by overcrowded conditions or where excessive hunting of ivory-bearing bulls has left only a number of younger bulls of equal status in the herd. She also speaks of "sire bulls" that she evidently considers are permanently attached to particular cow/calf groups and infers that "any decline of physical vigour in the sire bull must ultimately result in his displacement by a stronger, large, up and coming senior contender for his position as 'A' bull of the herd". As she presents no hard evidence, these statements, which were made before precise information on individually recognizable animals became available, must be conjectural. The Manyara evidence did not reveal any such permanent relationships between bulls and family units.

Anti-predator Response

As a result of my need to approach individuals frequently as part of the population study, I was the subject of many threat displays and observed many avoidance responses. Lions, Hyenas, Buffaloes and Rhinos were often met by similar displays and I will give a generalized description of these responses and refer to animals which elicit them as "potential predators".

Undisturbed elephant may be engaged in a wide range of activities such as feeding, drinking, resting, scratching, wallowing, walking or playing. Often the first sign that elephants have become alerted is that they stop their current activity, becoming motionless. There is usually a short period of 5 - 60 seconds when they become absolutely silent and obviously attempt to locate the source of disturbance presumably using all their sensory abilities. Trunks customarily hang straight down motionless, unless there is scent on the breeze, in which case they shift the tip in an arc around their heads. When alert the ear tips are slightly cocked up above the level of the shoulder blades but only half extended forwards. Elephants in this posture react quickly to any suspicious noise swinging around to face it. It is possible that these attitudes of trunk and ears, and the cessation of activity and vocalization, may act as signals to nearby elephants that danger is at hand as suggested by Buss (1962). Certainly the speed with which a complete group can respond to a single alien stimulus, visual, olfactory, or auditory, suggests that individuals become alert to the response of others even if they themselves have not perceived the original stimulus.

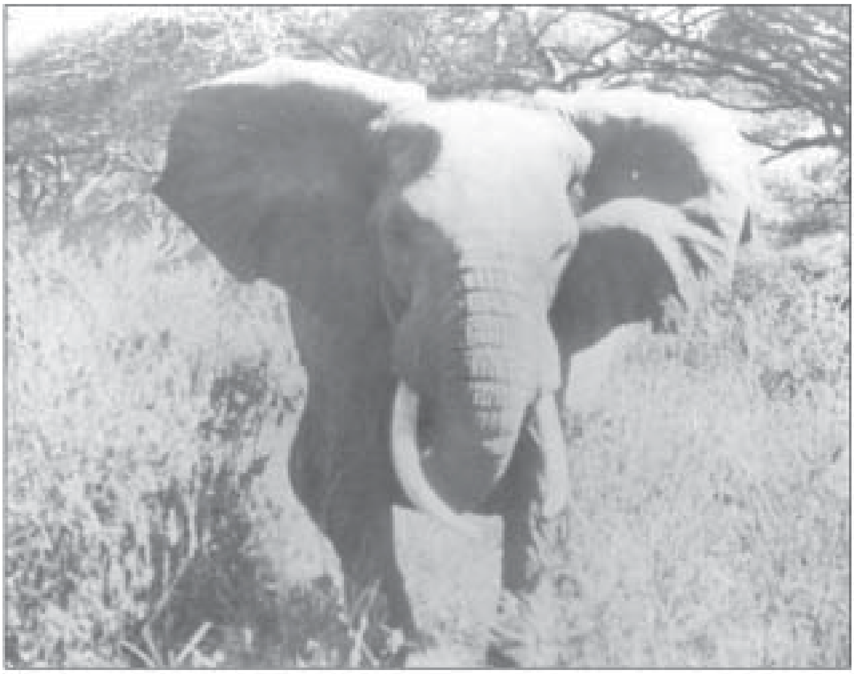
Following this the elephant may charge. In a charge, the trunk is almost always rolled back; the head may be high or low. The ears are always maximally extended. The elephant may trumpet as it charges, but trumpets are usually withheld until they halt. A usual sequence of events is as follows: the elephant begins with head high and then directs its course to pass through bushes. As the bushes are approached, the head is lowered and then jerked up so that the tusks scythe through the bush, creating a great deal of noise and demonstrating to the 'potential predator' and certainly the observer the force of the elephant's aggression. If the potential predator' remains stationary, the approaching elephant is forced to decide between full attack or a halt and further static threat display or a retreat. Almost invariably an elephant charging a car comes to a halt but I observed three charges which developed to the stage where elephants actually hit my vehicle and two similar incidents happened to tourist vehicles while I was in the park. In every case, the animals were cows, although many attacks by bulls have been documented elsewhere in Africa (Bere, 1966; Dr. L. Van den Berghe, pers. Comm.).

All out attacks

A feature of serious attack is that the threat display is often reduced or absent. An example of a group in attack is recorded in my field notes of September 18th, 1967. I approached an unknown group in an area of relatively thick scrub in the South of the park.

> One unknown young female with new-born calf disappeared to the right. After a 60 second interval, a large female (size category 5), with ears fully extended, charged silently out of the bush into which the young female and calf had vanished. She forced one tusk into the side of my landrover behind the cab without checking her stride. The vehicle was turned through 90^0. Now other elephants appeared, which prevented any further observation of the first cow, but from the damage it appears that she had withdrawn her tusk and dealt one more blow.
>
> The new elephants with a calf of about three years among the foremost came

Figure 6.21
Anti-predator response



A. **A charging matriarch before hitting Landrover. Note coiled trunk.**

B. **Charging bull before killing running figure. Note extended trunk.**

Photographs by courtesy of Dr. L. Van den berghe.

> running from the right hand side and went straight into the attack without any hesitation but this time the action was mingled with loud, continuous trumpeting. A second fully adult female used her head to butt and afterwards press down upon the roof of the cab. She leaned heavily sideways against the vehicle and her tusks scraped the bodywork behind the door. A third large female charged from the foot and drove her left tusk through one of the headlights. She withdrew it rapidly and thrust again penetrating past the radiator until about $3^1/_2$ feet of the tusk were buried in the car. She jerked up her head let it return and began to push. The car was moved backwards for about 35 yards until it hit a small tree. The third cow and the others now retired for about 30 yards where they stopped and formed a tight circle, still trumpeting, and facing outwards with ears spread out and heads lifted. Within the next, minute the group dissolved into the bush.

The silence of the first attacking female was unusual. The lack of any hesitation in her attacks contrasted strongly with the normal threat behaviour of the Manyara elephants observed up until then. A possible explanation is that elephant threat displays are derived from conflict behaviour and in this example conflict was lacking.

The two other attacks that resulted in physical contact varied in certain details. In the first a matriarch trumpeted and made one threat charge before attacking, and she did so in isolation to the rest of the group. (Fin. 6.2l A). In the second example a matriarch once again acted in isolation after a prolonged group threat display during an immobilization operation. When charging smaller animals the trunk may be directed forwards as in Fig 6 .2l B, a photograph kindly provided by Dr. L. Van den Berghe, who informed me that the bull elephant caught up with the individual seen running away, smacked him down with its trunk and then tusked him in his head. The bull was later shot and an old bullet wound was found; so this may truly be described as an anti-predator response.

However, such full attacks are very rare. If the ‘potential predator’ remains motionless, the elephant will usually pull up to a halt between 5 and 20 metres away, stand tall with ears out, possibly swish the trunk forward from its coiled position and peer over its tusks. The trunk swish is usually accompanied by a trumpet or forcible branchial expiration. The trunk then hangs straight down or slightly backward.

If the elephant is a solitary bull, or a cow which has isolated itself by more than 50 metres from its group, the threat is most likely to develop immediately into retreat. (Fig. 6.22 A - E). If the animal has companions around, it may enter a phase of attack - withdrawal conflict which has many elements.

Retreat

In retreat the head is held high, the back is arched and the tail is raised. (Figs. 6.22

Figure 6.22
Bull threat display followed by retreat

A. **Charge.**

B. **Standing still.**

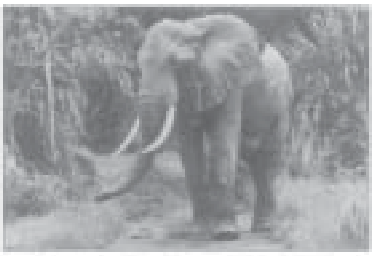
c. **Turning.**

D. **Turning.**

E. **Full retreat**

Figure 6.23
Bull retreat sequence

A. Undisturbed.



B. Alert.

C. Spotting a predator.

D. Standing still.

E. Turning.

F. Full retreat.

E, 6.23 F). The ears, although still cocked so that the upper edge stands above the shoulder blades, are no longer extended frontally. While retreating, the elephant usually bends its head to the side and moves at a slight angle from the straightest line of escape, so that it can look backwards at the 'potential predator'.

In some cases elephants which have been badly disturbed will move quickly to another area, walking 10 – 30 kilometres in 24 hours. I observed this happen after immobilization operations to family units both in the Tarangire and the Serengeti National Parks. In each example the experimental animal was a young bull still attached to a family unit. Croze (pers. Comm.) records a third similar example. In Manyara however, no changes of range were noted after any of the 14 immobilization each of which was followed up thoroughly. The Manyara sample included adult and immature bulls, calves and one adult cow. I attribute this tranquility to their relatively high degree of habituation to human stimuli.

Conflict behaviour, 'Irrelevant Activity'

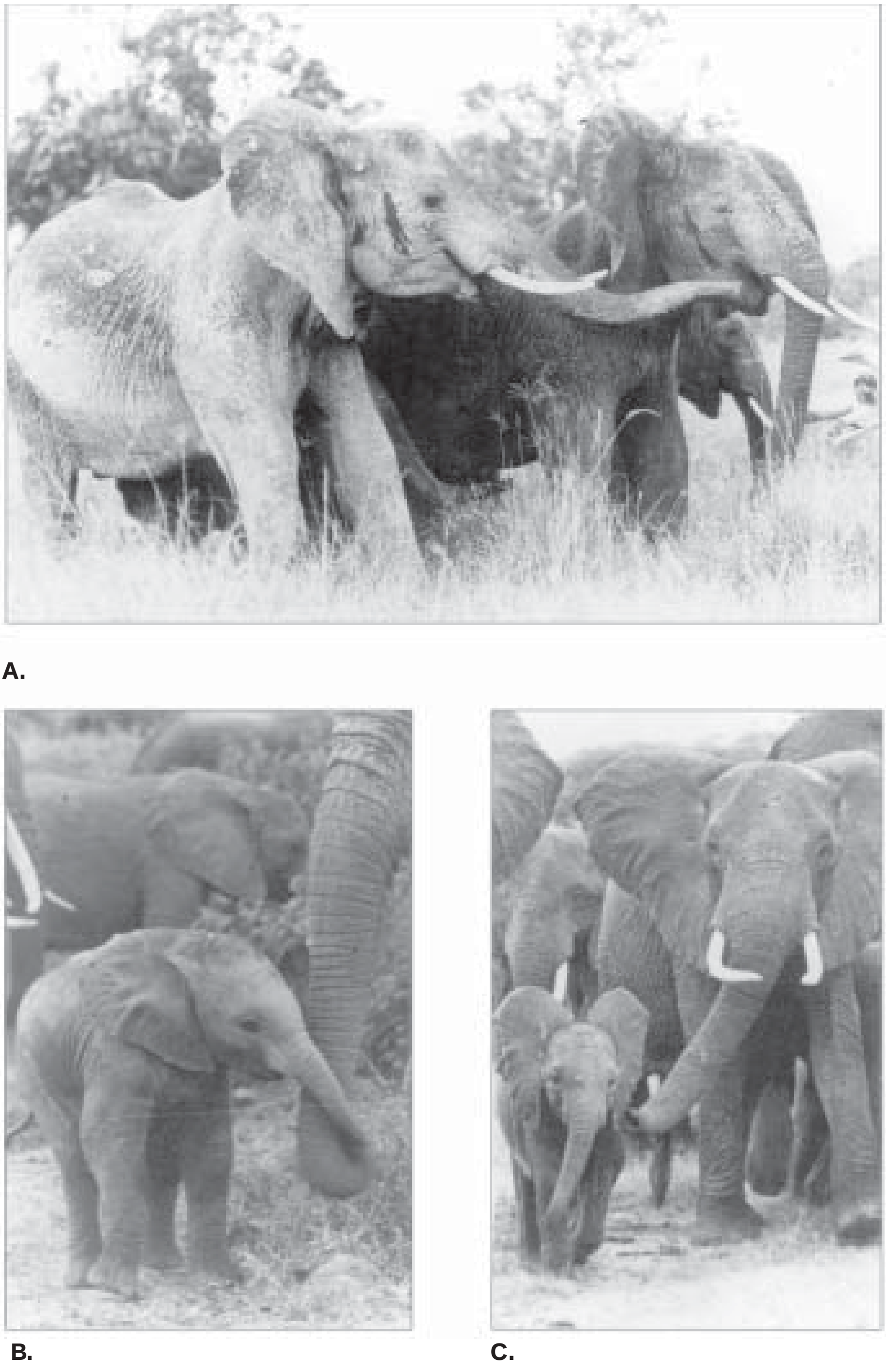
After the initial alert or following the threat charge a period is commonly entered in which the elephant engages in many apparently irrelevant activities such as throwing dust, swinging a foot, rubbing an eye, or swaying from side to side. Grass may be pulled and the normal feeding sequence, which involves shaking the grass free of soil by slapping it against the foot, becomes exaggerated. These 'irrelevant' activities are combined with elements of threat. For instance, an elephant might pick up a trunkful of dust and hurl it into the air at the same time jerking the head up and extending the ears.

In an ambivalent mood the trunk is particularly mobile, coiling and uncoiling, writhing and swinging. Similar conflict trunk movements were described by Rensch, when his experimental elephant was confronted with, a difficult choice in laboratory discrimination tests. The more agitated the trunk movements appear to be, the more likely it is that the elephant will retreat.

Conflict behaviour and mild threat is more commonly seen when elephants are in groups. Each elephant is influenced by its companions and the first animal either to increase the level of aggressive activity or to break into interest is likely to be followed by others. Growling or trumpeting by one is likely to stimulate a flurry of growls and trumpets from other group members. The larger cows usually take the initiative.

Some forms of tactile interaction between the elephants may often be seen among alarmed elephants such as leaning heavily together or rubbing flanks. On some occasions the heads are swung up together, and the elephants turn towards each other inserting their tusks in each other's mouths and often clashing their tusks, all the time keeping an eye on the 'potential predator'. Figure 6.24A illustrates the beginning of this sequence.

Figure 6.24
Reassurance behaviour



Three examples of trunk contact ic moments of stress which appeared to calm the recipient.

Often this display can involve more than two animals. Several cows stand in line and swing up their heads clashing each with its left and right neighbor. It is an impressive display to an. observer, but the gentleness of the trunk movements, which make tactile contact either on the forehead or in the mouth, suggest reassurance rather than redirected aggression, although several of the characteristic elements of aggression may be present. This display almost always seems to calm them and to diminish flight tendencies. Sometimes however it may be followed by further aggressive activity manifested in prolonged growling and trumpeting. The slightest sign of withdrawal on the part of the ‘potential predator’ may now elicit a further advance or full charge.

> One family unit, AET, was particularly prone to delayed aggression after group reassurance, and on seven separate occasions made a group threat charge after stationary threat and reassurance that lasted from 5 to 25 minutes. On two occasions renewed threat charges ended in minor physical contact between an elephant and a tourist car. In each case the drivers had remained stationary during the first dummy charge and lingered to watch the conflict and static threat behavoiur. Tactile reassurance amongst the elephants led to heightened aggression, putting the tourists to flight, and the elephants pressed home their attacks by tusking the rear ends of the two vehicles.

Tactile interactions in these situations may also commonly be seen between adults and calves. A cow or elder sibling may restrain a calf with a trunk or gently touch it, rub it with a foot, or embrace its trunk (See Fig. 6.24 B,C).

In captivity elephants are temperamentally liable to panic when confronted with unusual stimuli (Hediger, 1950), but older animals often soothe disturbed juveniles by gentle tactile contact of the sort seen in the wild. (Mr. R. Chipperfield, pers. comm.). I have observed wild elephants injure themselves when retreating by rushing into rocks or tripping and falling to their knees. Primitive hunters are thought to have stampeded elephants over cliffs (Carrington, 1958). Clearly blind panic-stricken retreat is non-adaptive. A social signal in the wild from an experienced elephant, which prevented younger animals from unnecessarily running away, would have great survival value, and this seems a likely function for the tactile exchanges described above.

Group Defence and Mutual Assistance

Bulls may go through the whole gamut of threat displays conflict and irrelevant activity, but their behaviour tends to resolve itself more swiftly than the group-conscious females.

Bulls are unlikely to turn at bay in the open once they have began to retreat unless they are closely pursued. I never observed any co-ordination in male groups in attack or retreat, nor did I record ‘reassurance behaviour’ as described for females. Their response could usually be summarized as ‘every bull for itself’. However reliable accounts exist that bulls do occasionally assist others that are wounded, by lifting them to their feet, and pressing in from all sides to prevent the wounded animal from falling. (Dr. H. Lamprey, pers. Comm.).

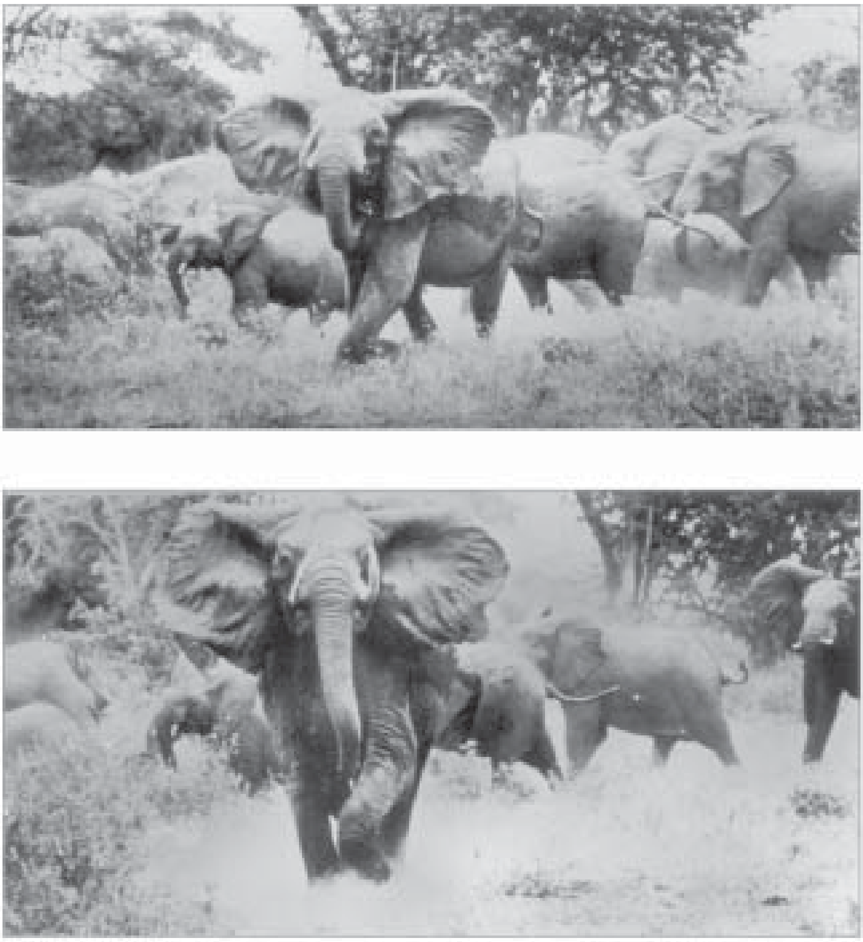
It is widely asserted by hunters that when a bull becomes old and feeble with a heavy load of ivory to carry around he is attended and protected by certain young bulls, popularly known as ‘askaris’ (askari is the Swahili for guard) This view receives support from Sikes (1971) who asserts that sometimes these senile bulls have one or two younger bulls in permanent attendance”. The documentary film ‘King Elephant’ (1972), refers to ‘Ahmed’, the well-known bull of Marsabit mountain in the following words: like squires, younger bulls await the call of ‘Ahmed’, the largest of them all”.

As it has been shown in Chapter 5, observations of bull associations in Serengeti (Hendrichs, 1971; Dr. H. Croze, pers. Comm.) and at Manyara did not support these assertions. However, since in the Manyara and Serengeti study areas big bulls were either absent or extremely rare, final investigation of this legend must be made through observations of old bulls. The movements of ‘Ahmed’ have been regularly noted since 1956 (Fig. 5.21). Mr. B. Woodley, a former warden of that area from 1961-1969, has told me that on many occasions he has seen ‘Ahmed’ in a company with cows or other bulls young and old but these associations were most irregular. He never noticed any recurrent associations between ‘Ahmed’ and any other distinctive bull, that struck him as significant, nor did he notice any behaviour suggested by the askari concept.

It seems therefore that there is no evidence to support this belief which probably originates from the experience of hunters who when trying to get close to an old tusker with heavy ivory, have been charged by a younger, probably more alert bull in temporary association. However a threat charge is part of any elephant’s defensive repertoire, and the behaviour of the younger bulls can be explained in terms of self-interest rather than altruism.

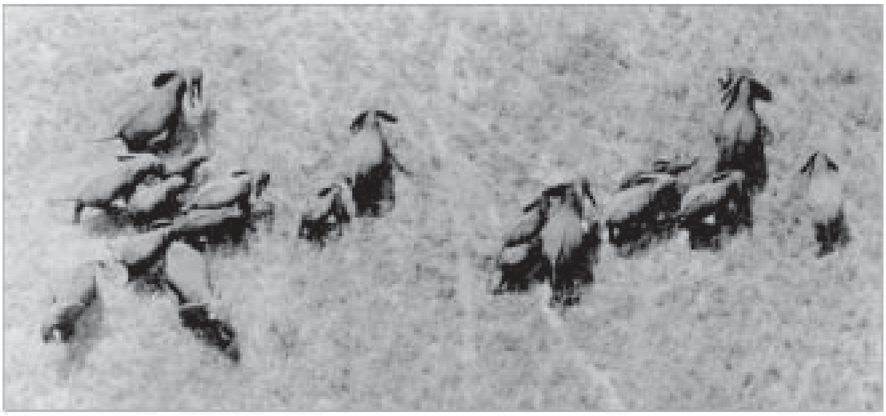
In contrast when a family is caught in the open they bunch together and large females move to the circumference facing outwards while the calves and immatures face into the centre (Fig. 6.26 A- C). If the threat becomes from one side the large females tend to concentrate on that side. This circular clump of elephants moves in tight formation and when in retreat one or two females usually take up a rear-guard position. The most active female in defence is usually also the largest, the matriarch. She may meet the threat from whatever direction it comes making a threat charge while the rest of the group escape, Fig. 6.25 - A- C, In retreat she will adjust her pace to the slowest calf’s movement. The group withdrawal with-rear guard action by the matriarch is typical of open conditions. In closed areas with thickets for cover, the probability of more aggressive group defence is greater.

Figure 6.25
Group defense: Matriarch threat display while family unit escapes



Note apparently “irrelevant” foot swinging.

Figure 6.26
Group behaviour: Formation of a circle



A. **Two family units of one kin group bunch when alarmed. Note two females (lower left) act as rear guard.**

B. **Denfensive circle with tuskless matriarch.**

C. **Denfensive circle. Note calves facing inwards.**

Groups in defence may be composed of several family units. These are most likely to be related members of a kin group, but they may also be strangers. Certain stimuli, such as calf in distress appear to release protective behavoiur even in unrelated elephants.

One co-ordinated defensive interaction I observed involved five separate family units, occurring during five separate immobilization in December 1967. Two of these family units, VIC and FLO, belonged to one kin group and the remaining three family units, BOA, LEO, and JEZ belonged to another kin group. Although all these family units met each other frequently, any relationship between the two kin groups must have been distant.

I selected for immobilization a young male of about 8 years, known as Mary's C2 in VIC F.U. This unit was
a cohesive highly integrated group with 5 mature females and has been used in Chapter 5 as an example of family unit integrity.

At 16.46 hours the calf was injected with a solution of 4 mgm. of Oripavine hydrochloride (Reckitts and Coleman). At that moment VIC F.U. was leading, and slightly to the rear was FLO F.U. B0A, LEO and JEZ F.Us were approximately 150 meters away walking in parallel, through open Acacia tortilis woodland. The relative position, degree of inter-mingling and numbers of each family unit are sketched below:

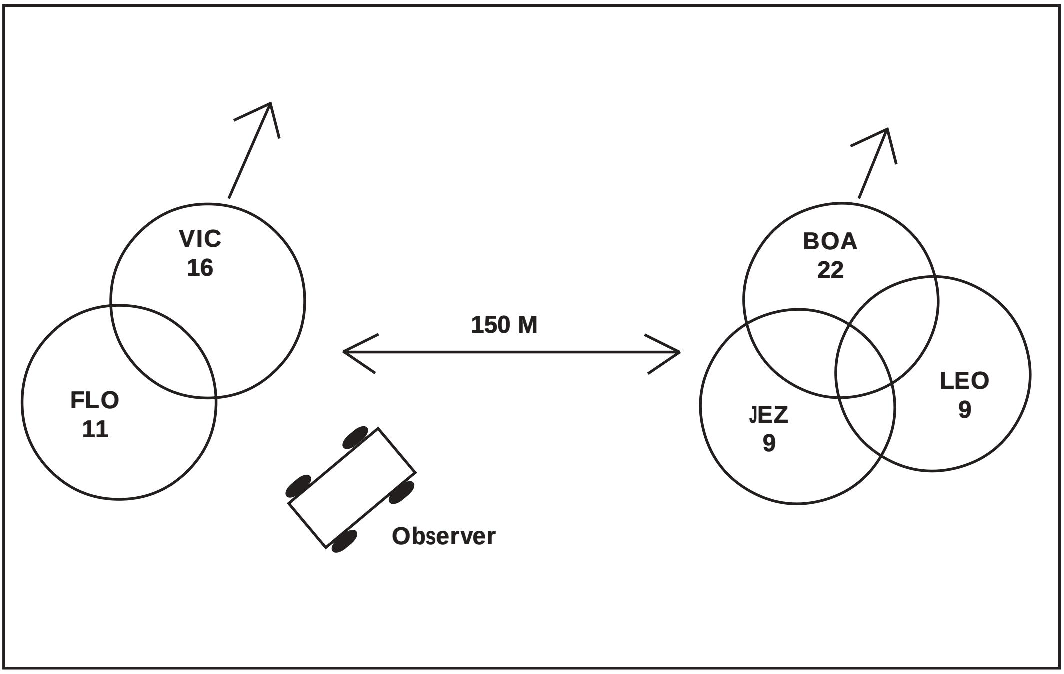


Figure 6.27
Protective behaviour

A. **Palaeolithic rock engraving from Ain Safsad, Algeria, shows mother defending her calf from a leopard**

B. **Cow lifting immobilized calf.**

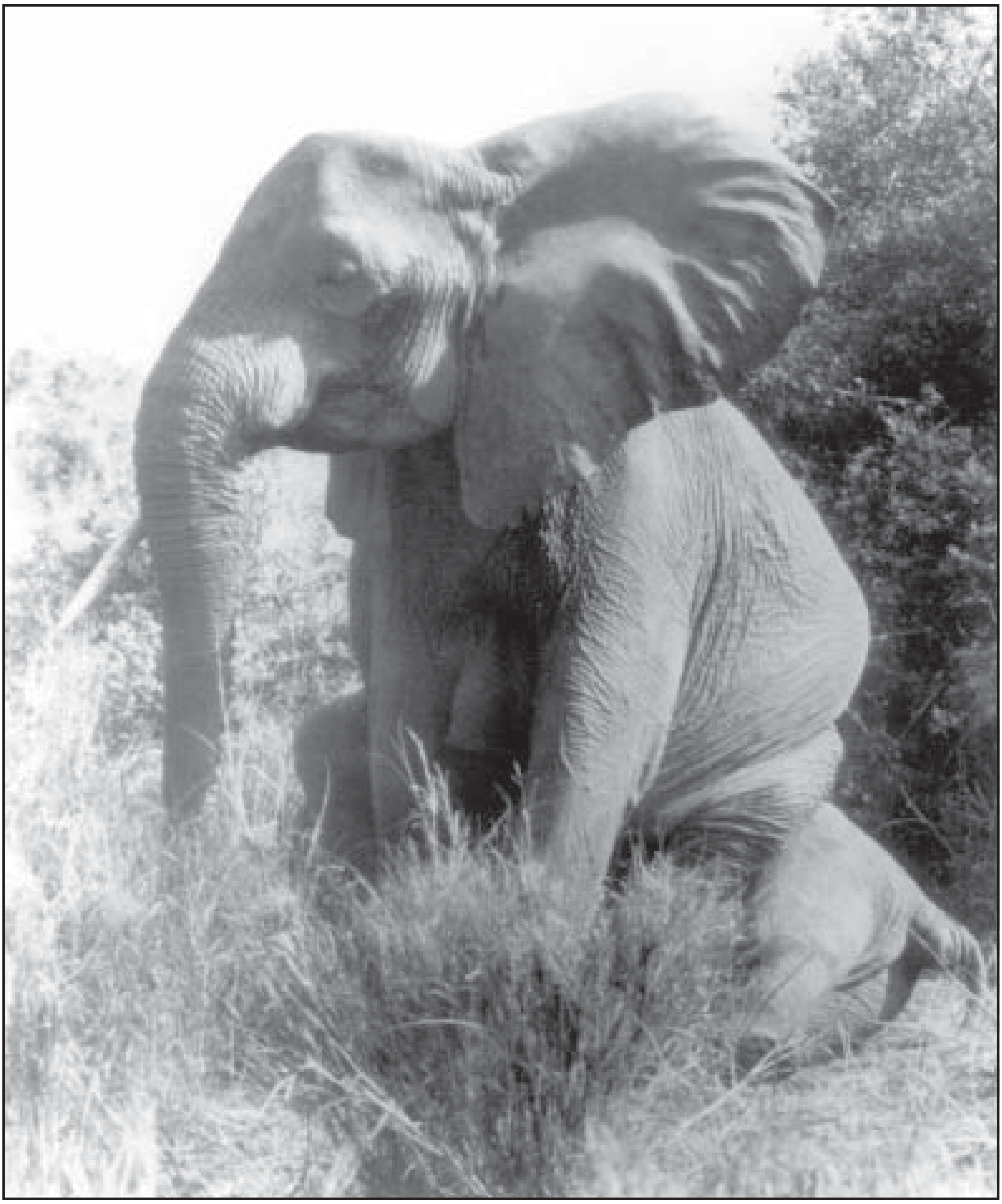
(A. By courtesy of the Musse de l'Homme, (Cliche: Oster) Paris).

The syringe dart struck the calf in the loose skin below the armpit, apparently biting an insensitive spot, as it neither checked its stride nor made a noise. The discharge of the CO_2 'Capchur'' gun caused virtually no disturbance. One adult cow, Kali Ears (a female from VIC F.U.), swung her head in the direction of the noise, but then with the others continued to walk steadily at the same pace and in the same direction as before. A summary of my field notes describes the subsequent behaviour:

> "Darting **+** 12 minutes: the calf suddenly keels over flat on its side after walking quite normally. Immediately the nearest cow, Mary (his, mother), swings round and trumpets. She rushes forward to investigate, extending its trunk in its direction. Other cows all turn around and surround this calf, with their ears forward and heads down, trumpeting and growling. Anna (female from FLO F.U) looks in our direction but appears to decide that we are not connected, as she makes no demonstration. Loud trumpeting and growling continues. BOA, LEO and JEZ F.Us charge over on a broad front to join VIC and FLO around the fallen calf. I try to head off these groups but only succeed in stirring them up to a tremendous demonstration. For a few minutes they are behind bush. Then I can see Kali Ears and Mary trying to lift the calf while Victoria (the matriarch of VIC F.U.) paces back and forth between us and them. The calf never loses consciousness and his trunk moves up towards these great mothers each time they try to lever him into a standing position. They will not leave him alone. Their movements are violent and they jerk him upwards. Each of the three cows makes an attempt in turn or together (Fig. 6.27B). They lean their bodies together at acute angles and form a solid wall between us And the calf. BOA, LEO and JEZ F.Us join in the activity of guarding this calf, intermingling with FLO and V1C F.Us. repeated attempts to drive them away fail. I withdraw to watch from a distance. Trumpeting, growling, shrieking and moaning continue intermittently. A pall of dust has been thrown up into the air.
>
> Darting **+** 45 minutes: VIC and FLO F.Us (the parental kin group) wander away from the calf apparently leave it. BOA, LEO and JEZ F.Us. remain guarding it. After another 45 minutes I see Mary and Victoria reappear. They resume lifting the calf and it begins to raise its forequarters with their help, every so often collapsing back again. Disturbed trumpeting and dust throwing continue at a reduced level. All five F.U's are once again a huge intermingled conglomerate.
>
> Darting + 2.05 hours: Finally the calf gets up on all legs and stays up. It is now very dark and I leave.

Two aspects of this interaction are remarkable. Firstly aid was given by elephants not closely related to the distressed calf, which initially responded to the alarmed trumpets and growls of the adults of the parent kin group of VIC and FLO F.Us. Secondly the calf was abandoned and left in the protection of

Figure 6.28
Unexplained behaviour caused by immobilization. Cow sits on drugged calf belonging to unrelated family unit, after her attempts to raise it had failed.



(Photograph by courtesy of Mr. Simon Trevor).

the strangers for about 45 minutes. Either of these observations, in isolation, might seem insignificant, but I recorded interaction similar in these two respects one and a half years later:

> "This time, in July, 1969, I immobilized an 8 year old male of ASS F.U. There were only two adult females in this group, Assym Ears, the mother, with three calves, and Arene with none. From the moment that the dart struck I was able to watch unimpeded from 10 metres. Once again the elephants seemed quite unaware of the cause of the calf's distress and made very little threat towards the landrover. From field notes:
>
> > "Calf goes down -"Assym Ears and Arene swing round to its assistance. Arene pushes with her forefoot while Assym Ears attempts to lever him up with her tusks, both females trumpet and growl. JEZ F.U. rushes over from 200 meters and the three large cows of this F.U. chase Assym Ears and Arene away from the recumbent calf (There were altogether 12 numbers in JEZ F.U). The strange females now try to raise the calf with trunk and feet. After three minutes they all loose interest except one, Curie. Finally after all her attempts at raising the calf fail, she sits on top of it with all her weight (Fig. 6.28). Faeces are squeezed out of its anus under this pressure.
> >
> > Six minutes from darting, Curie leaves the calf and it is now totally abandoned. I inject the antidote.
> >
> > One minute later Assym Ears, the mother, and Arene reappear. They resume lifting. The calf is raised to its feet and stands shakily. Arene places her trunk in its mouth then caresses its forehead. The two females continue to keep close to the calf, one on either side, for the next hour, after which it seems completely recovered."

The display of aggression by a strange F.U. towards the parental FU is not worthy in this instance. Both the inter-group aggression and the female sitting on top of the calf appear to be curiously irrelevant' activities.

A similar observation has been made by Croze (1971, Life Magazine), who described how a bull performed a pseudo-copulation with a dying cow after first attempting to raise it. Croze's observation is also interesting as an example of a bull engaging in the 'altruistic' activities usually typical of cows.

The apparent altruism which I have described between F.U.s with little or no blood relationship can probably be explained as a generalized response of individuals to the stimulus of a distressed elephant. Genes which tend to increase the probability of an elephant behaving in this way would tend to perpetuate themselves, providing the response were usually directed towards a close relation with those genes in common. The nearest neighbour data suggests that in cow/calf groups, a stricken animal would usually be surrounded by its close relations.

Likewise families of a kin group are likely to be in a position to give mutual aid.

In the course of immobilization operations I observed mutual assistance on a further nine occasions. The persistence with which the elephants defended a fallen one varied greatly, but the younger the calf the more strenuous the defence was likely to be. On one occasion the mother, a young cow, remained alone while the family unit retreated, on another occasion the matriarch stayed in defence while the family unit retreated. In one example in the Tarangire, a family unit made no defence at all but abandoned an 11-12 year male where he dropped. In the one case where an adult cow was immobilized the matriarch made one dummy charge and then abandoned the fallen cow as did her 8 year calf. It seemed that the wilder the group the less time they were to spend exposed to the 'potential predator' even if one of their number was recumbent. In the three cases, from southern Manyara, Tarangire, and Serengeti the defence was either absent or perfunctory. These three areas contain elephants which normally react with extreme fear to man and which are presumably shot at from time to time.

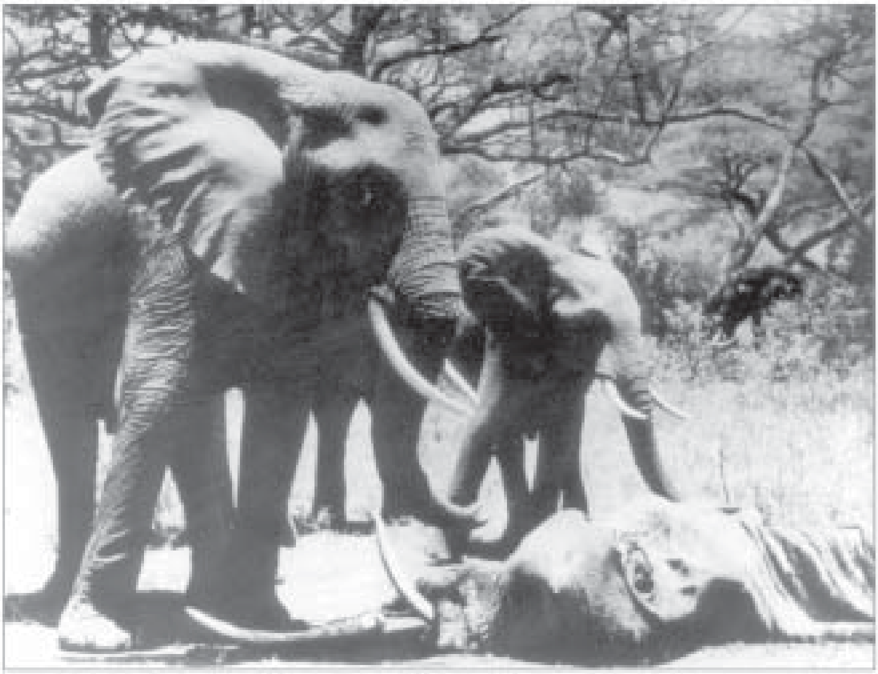
Lions and hyenas occasionally attack elephants. In March 1966 I observed a large male lion on the scattered remains of a six-month calf which had been seen wandering alone the previous evening. Some visitors camped nearby told me that they had heard sounds of a struggle in the night, with the elephant squealing, bushes breaking, and the lions growling. Lions have also been observed attacking isolated half grown elephants (Selous, l88l; Mr. S. Trevor, pers. comm.; Sheldrick, 1972). I have been unable to find any record that lions will attack a group in order to cut out a calf, in a way similar to the description of a tiger attacking an Indian elephant for this purpose by Williams (1953). A Paleolithic rock engraving at Ain Safsad in the Sahara illustrates a cow defending her calf from a leopard (Fig. 6.27A; Musee de l'Homme, Paris.). Hyenas have also been cited as elephant predators (Bere, 1966; Anon, 1971, Africana 4).

In most circumstances, elephants are characteristically tolerant of other animals. However they do react strongly to moving lions and hyenas. I once observed a cow/calf group forming a defensive circle, when two hyenas trotted past them at 150 metres on an open river bed. Two cows chased the hyenas away. A similar interaction in which females of F.U. chased wild dogs away has been observed by Mr. S. Trevor and appears in the film 'King Elephant' (1972).

Moving lions provoke a similar reaction, and I have seen family units charge a pride of lions on a broad front on several occasions. It is only necessary to imitate a lion's call to provoke this response. Makacha and Schaller (1969) record an incident in which a group of elephants of Manyara killed a lion cub by stepping on it, after the rest of the pride had run up a tree, presumably to escape the elephants. On other occasions when lions were up trees elephants passed directly underneath without making the least demonstration, even though they raised

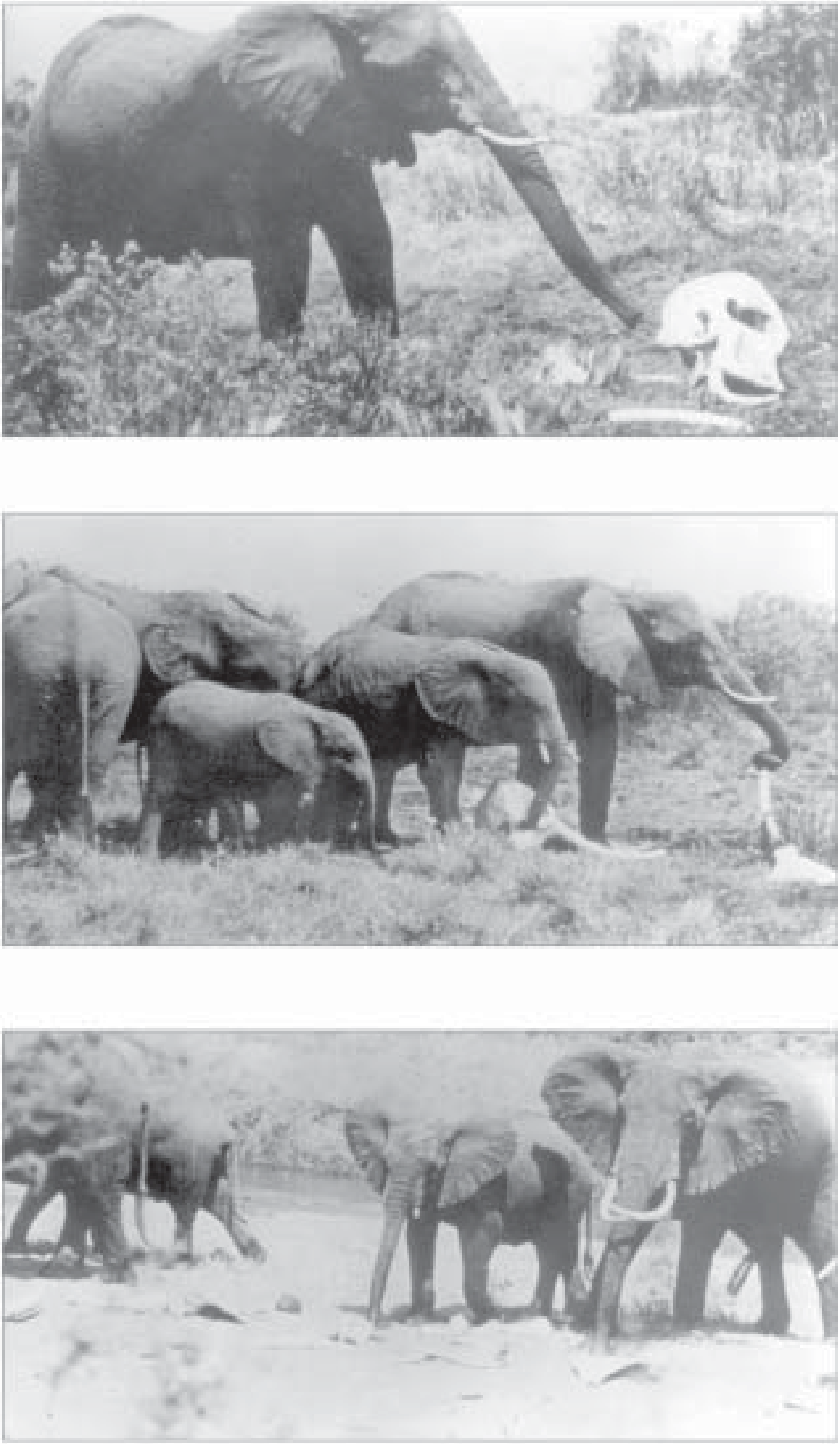
Figure 6.29
Behaviour towards elephant carcass

A. **CLY F.U. approaches the corpse.**



B. **Melanea and others investigate the corpse before moving on.**

Figure 6.30
Planted bones and tusks elicit interst from cows and calves



their trunks to sniff at it, indicating that they were aware of its presence.

Behaviour towards Dead Elephants

Attempts to assist a dying elephant may continue after it is dead.

> "In March 1970 I found a freshly dead cow which had fallen off a trail leading up the precipitous Endabash escarpment. Trees which had stood in the path of her fall were broken, and I later backtracked her descent to a point 130m up the slope. Here I found her last footprints. It appeared that she had stepped into a pig hole covered with vegetation lost her balance and rolled over out of control down the slope. Her neck was bent backwards at an acute angle and was probably broken. She appeared to have died only as not many flies had settled on her body.
>
> When I arrived three calves, aged approximately 9 months, 4 years and three years were at her side and the oldest bellowed at least once every 15 seconds. From time to time it made attempts to lift the dead cow with its trunk and tusks and was assisted by 4 year old. The youngest calf tried to suck twice. After 15 minutes they caught my scent and slowly walked away down the escarpment."

Similar behaviour has been described by Croze (1971, Life Magazine) who observed several members of a family unit and one bull attempting to raise a dying cow, and continuing their efforts even after she was dead. Mr. B. Woodley observed cows and calves defending the dead body of a young female for three days after it had been shot. Bere (1966) recorded that a cow carried the body of its calf for several days after the calf had died. Winter (1964) described how about 30 elephants remained with a shot cow, one of them even breaking her tusks in an attempt to lift the dead animal.

Such a responsiveness to inert individuals is of obvious value in saving a member of the group which has temporarily collapsed. The individuals which save it might well benefit after the sick animals recovery, by its taking part in the defence of calves, or if it were a matriarch by her experience in finding food and continued leadership in times of stress.

More difficult to explain is the interest which elephants may show even in corpses which have almost completely decomposed.

> "In June 1970 while watching some vultures on the corpse of a cow of TQR F.U., that had died three weeks previously, I saw a cow named Clytemnestra, the matriach of CLY F.U. appearing about 30 metres away with her group close behind her. She caught sight of my vehicle, extended her ears, looking sideways in my direction, and then continued along the same path. Then quite suddenly she extended her trunk together with the others and sampled the air. Evidently they had just detected a scent coming from the

> direction of the corpse and myself. Clytemnestra immediately turned to walk straight towards the corpse behind which my car was parked with heads up and ears out, three members of the group came right upto the corpse and began investigating it with their trunks. They touched the bones picking up some and tossed them aside, and moved the tips of their trunks under the skull, skin and tusks for about three minutes (Fig. 6.29 A-B). Then one of the younger cows, Melanea, made two paces in my direction, stood tall, shook her head, and passed on followed by the rest of the group. This incident brought the group nearer to my car than they previously had been in 38 observations, and it seemed that they initially changed course in order to come and investigate the corpse rather than to make a threat display at the vehicle."

Subsequently I transported one complete elephant carcass to a place where elephants came to drink; and waited to observe their response. Out of eight more approaches on two occasions cow /calf groups walked right over the bones without paying attention at all. On one occasion two bulls played their trunks over the bones, touching and presumably smelling them for about one minute. On the remaining five occasions cow/calf groups approached the remains and exhibited excitement, by raising their tails and slightly extending their ears. Some picked up bones and tusks, others merely smelt them (see fig 6.30 30 A"– C). I concealed downwind and remained apparently undetected on each occasion. Although these experiments were crude, and human scent left on the bones could not be eliminated as a factor, I was left with the strong impression that the bones held some special significance for the elephants and that this behaviour would not have been displayed towards other inanimate objects. Mr. S. Trevor has also observed, filmed, and Photographed, similar behaviour on many occasions. ('King Elephant', 1972; pers. Comm.).

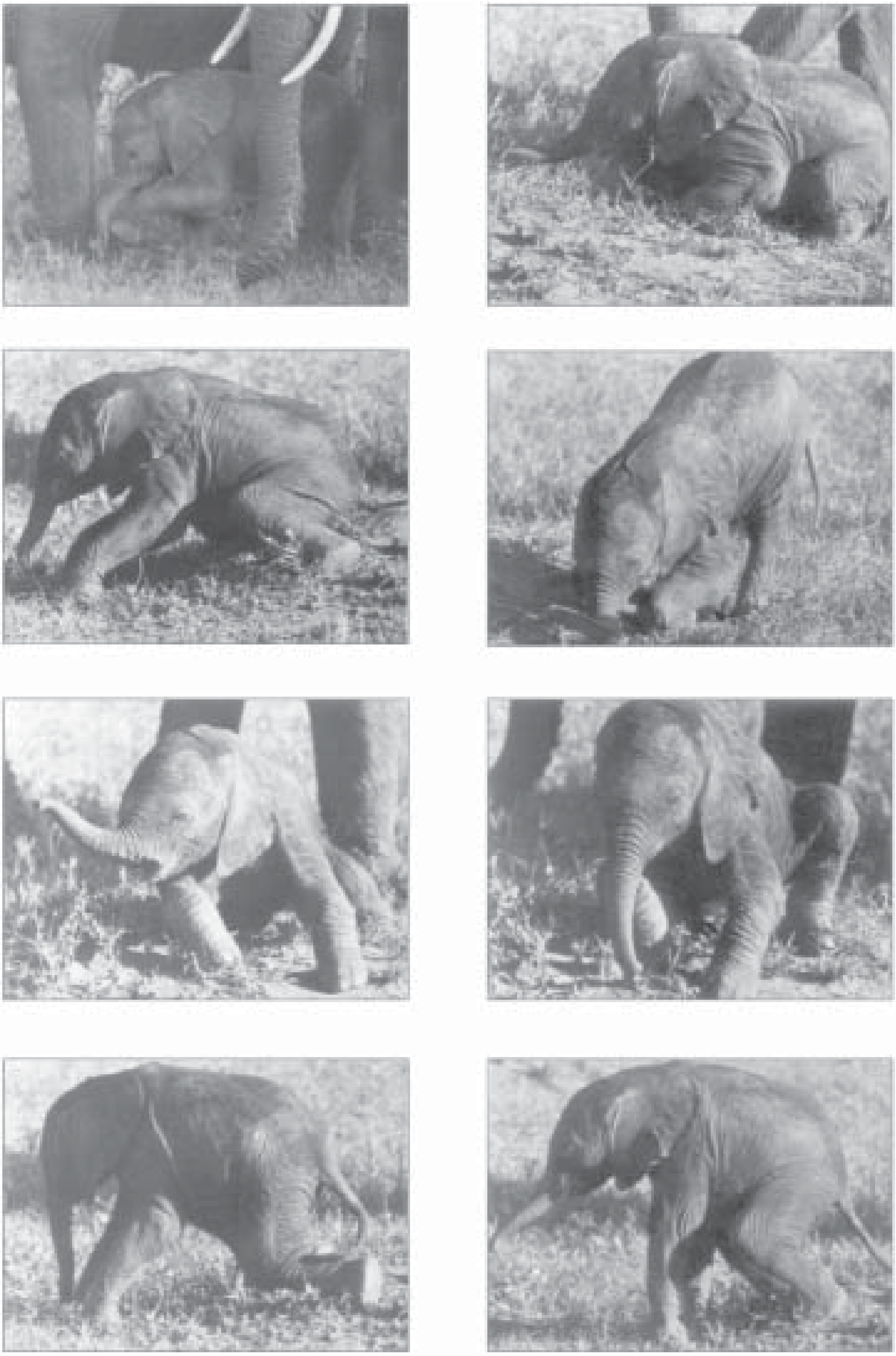
The buying of corpses, or the covering of them with leaves has also, been widely reported (Verheyen, 1954; Grzimek, 1956; Guggisberg, 1956; Adamson, 1968, Mr M. Turner, pers.comm.., Mr. A Root, pers. comm.) but I have never observed this behaviour.

In spite of the fragmentary and incidental nature of the evidence, it seems clear that elephants often show more than a passing interest in even totally decomposed carcases of their own species. One can only speculate about the survival value, if any, of this extraordinary behaviour. It could be merely an extension of the reported assistance to sick individuals, due to a scent lingering on even long after death, which remains sufficiently "elephantine" to elicit curiosity. On the other hand the olfactory exploration may provide information about how the animal died which could conceivably be of value, but at the present stage this must remain conjecture.

Learning and memory

It has been suggested that the prolonged immaturity of the elephant, as in man, is

Figure 6.11
Exploratory movements of three month old calf



one of the factors associated with the evolution of intelligence (Laws, 1970a). While field observations were necessarily unexperimental, much incidental behaviour supported this view.

The movements of young calves are clumsy initially. They are however very active and adopt many postures which adults seldom use. Fig. 6.11 shows a calf of about three months in a series of positions which it adopted within quick succession of each other in the space of a few minutes.

This exploratory movement is probably part of a process of learning to promote its patterns. It takes calves many months even years, to acquire the complete skills in the use of their trunks.

Even drinking with the trunk has to be learnt and calves less than one year old may be seen drinking with their mouths, (Fig. 6.12 B) Adults use combination of tusks, feet and trunk with great precision in stripping bark, picking up pods and digging holes. They learn to spray water with the trunk and to pull grass, cut it with their feet and shake it free of dirt. Much experience also appears to be learned socially as in play fighting, and in the maternal behaviour of young females. The appropriate reaction to danger also appears to be a learnt response. On four occasions young calves of 3 to 6 months approached my landrover and touched it, apparently unafraid. The same calves a year older were much more wary and like their mothers kept their distance. We have also seen how the older animals control the extent of alarm by 'reassurance' contacts, perhaps teaching the younger ones the appropriate response to each situation.

Even adults learn to adapt to new situations. For example, in many areas where elephants are hunted along the National Park borders, they tend to run directly into the sanctuary if disturbed, as if they knew where safety lay. They also quickly learned to avoid the electric fence installed at Manyara during this study. This sort of learning in every case is probably speeded up by individuals imitating each other.

In a long-lived animal the passing on of experience from parent to offspring is of obvious value. The response to certain rare events may be critical for survival. For example, in Tsavo severe drought occur at approximately ten year intervals, as in 1961 and again in 1971-72 when approximately one third of the elephant population died of starvation in one section (Sheldrick, 1972).

It is easy to envisage a situation where a family might survive due to the experience and leadership of the matriarch. Major D. Sheldrick (pers. Comm.) observed during the most recent Tsavo drought that the condition of the animals varied greatly from one family unit to another within the same locality, as if some had been more successful in finding food than others. In certain small areas the elephants dug up all 'Sericomopsis roots', one of the few remaining sources of food, whereas in other areas this species was virtually ignored. Sheldrick suggests that these variations may have been caused by differences in matriarchal leadership and food searching experience.

In one drought-stricken area on the Tiva river, elephants needed to move only 8 Km. up or down stream to find plentiful food, and yet most remained and died (Sheldrick, 1972). It is plain that a matriarch who knew where to move to find food at such a time would have been more likely to lead her family to safety, and perhaps some did.

It is also reasonable to speculate that a young cow which survived a drought in one decade might well survive another, even after the death of the experienced matriarch, merely by repeating the movements and feeding behaviour originally learnt from the old leader.

Although conjectural, these possibilities show a way in which social learning might perpetuate valuable ‘traditions’ within a family unit or kin group.

Marked behaviuoral differences between populations lend support to the concept of ‘traditional’ learning in elephants. In the Addo area in the Cape Province of South Africa, an attempt was made in 1919 to exterminate a small population of about 140 elephants (Achibald, 1955). By the middle of 1920 only 16 to 30 were left alive. The provincial administration then decided to proclaim the area a sanctuary in 1930, since when elephants have been strictly protected. The behaviour of the survivors has changed little however, and the Addo elephants have remained nocturnal and respond extremely aggressively to any human stimulus. Few, if any, of the elephants which were shot at in 1919 can still be alive, but their defensive behaviour appears to have been learned by their offspring, and even by calves of the third or fourth generation, none of which have suffered from human predation themselves.

In the Wankie Game Reserve in Rhodesia the elephants can only come to drink in the open at water pans, but they only do so after dark. Weir et. al. (1965) suggests that this behaviour also may have been persisted from a time when this population was heavily hunted. Knowing where to find salt also appears to be important to this population (ibid.)

At Manyara marked differences were obvious between family units. Most groups in the central area were habituated to vehicles and moved in the open by day. Family units living in the south however, seldom came into the open during the day and would immediately retreat into the thickets on hearing a car engine or on smelling human scent. They were usually either extremely aggressive or in full retreat. Amongst these wild groups younger animals followed the example of their elders, and in a sense behaved according to the tradition of their family unit.

Evolution of anti-predator response

The timidity and tendency of elephants to panic at the least unknown disturbance may seem surprising in view of their size and relative invulnerability to predators other than man. It has been suggested that the development of effective weapons by man is of far too recent origin for his hunting to have influenced elephant behaviour by natural selection (Ardrey, 1970). Even if this premise were correct, it ignores the formidable predators that were present during the evolution of the elephant family.

It has been suggested that the sabre tooth cat, the Megantereon, of the European Villafranchian fauna, with its very strong front paws and huge stabbing teeth may have preyed on relatively slow moving animals such as the rhinoceros or young mastodonts and elephants (Kurten, 1968).

Similarly the Pleistocene remains of scimitar tooth cats of the Genus Homotherium, were found in caves in association with so many teeth and bones of juvenile mammoths that they may have formed the staple diet of these cats (Kurten, l968, 1971). Both these cat genera were also found in Africa. In Europe, Felis spelaeus the cave lion, and Ursus spelaeus the cave bear may also have been elephant predators. In America, Osborn (1910) suggested that Aritotherium hapladon a giant bear and Smilodon the North American sabre tooth tiger may have been capable of attacking young mastodonts. All these predators were considerably larger than contemporary representatives of the Carnivora. It is reasonable to conclude from the fossil evidence that up to the advent of Man the probascideans have been subject to attack from dangerous predators which may well have provided the selection pressure necessary to develop the massive size, thick skin and huge armament of the present-day survivors. It has been estimated that even recently Indian elephants in some areas suffered 25 per cent calf mortality due to tigers (Browne in McKay, 1971).

Paleotological finds also suggest that man may have been hunting Proboscideans for at least 20,000 years despite the lack of iron age weapons. Maska (1886) described a camp of mammoth hunters at Predmost, Czechoslovakia, from which the bones of more than 900 mammoths were recorded. Mixed in with the ashes of camp fires and the chipped flint implements of Aurignacian man lay the remains of complete fauna. Bones of wild horses, reindeer, bison, musk-ox and aurochs lay in profusion but more than 75 per cent of all the bones found were those of the mammoth Mammuthus primizenius, which suggests that perhaps the human predators, like the scimitar cats, were Proboscidean specialists. Man may even have been responsible for the extinction of the woolly mammoth, the straight tusked elephant and some of the numerous New world mastodonts (Osborn, 1910; Kurten, 1968, 1971; Martin 1966).

Recent methods of hunting the African elephant, which do not rely on iron age weapons, include pitfalls (pers. Obs) stampeding elephants on steep hill sides until they fall out of control (Carrington, 1958), driving them into marshes where the get bogged down, and ringing them with fire (Bell,1923).

Discussion

We see therefore that the elephant has a long evolutionary history as a prey animal, and early man may well have begun to prey on elephants before the large Carnivora became extinct.

There seem therefore to have been two factors at work in the evolution of escape responses; firstly genetic selection exerted by fairly recent predators such as the large cats and the stone age man, secondly individual conditioning based on experience with man, which may be transferred culturally from generation to generation.

Elephants within family units, and family units within kin groups are well spaced to respond swiftly in mutual defence. The effect on a predator of a large number of family units suddenly crashing through the bush on all sides, some charging towards it and some running away, is likely to be confusing and alarming. Another effect of clumping is the lowering an individual's probability of being a victim, as has been suggested for other species, for example gulls, by Tinbergen (1953). It is tempting to conclude that the marked sociability of elephants above the family unit level is largely an anti-predator adaptation.

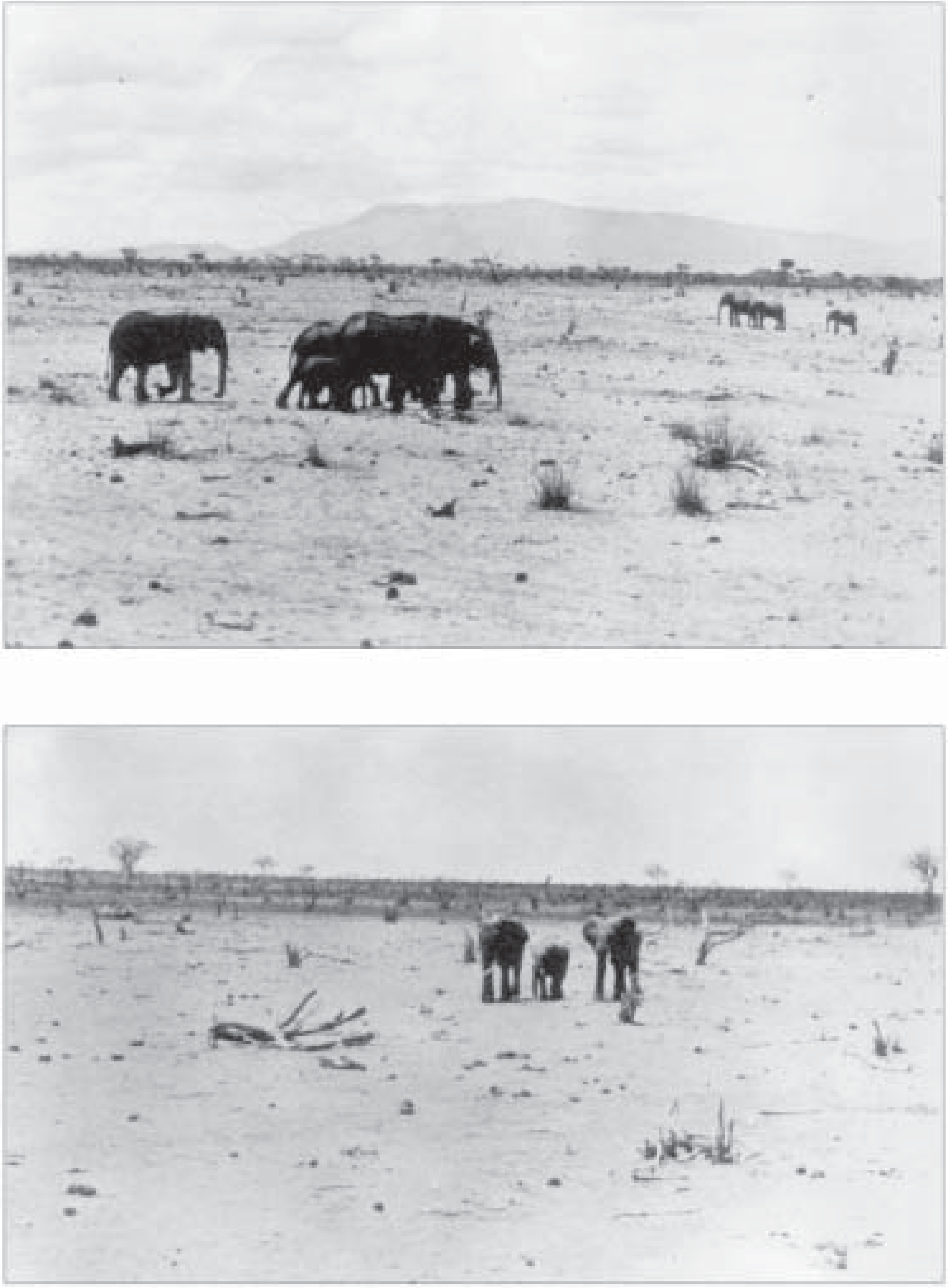
At the same time we have seen in this chapter that there are disadvantages in being near to other individuals particularly for elephants of low rank in the hierarchy. Competition within a family unit tends to lead to spacing and development of sub-groups. I would suggest that the young matriarchs in splitting from the old choose distances from the group that reduce the amount of competition and the likely hood of intolerant attacks from a dominant cow while not being so far away that they cannot benefit from the anti-predator protection of larger groups. Thus the young matriarch plus her group should be able to get their water, wallowing and feed without impediment and still be within earshot i.e. trumpet range of the others, should they run into trouble.

If predation and competition are the two major factors affecting elephant group sizes, then it would be expected that under conditions where the danger of predation was high, the groups would tend to be large; and under conditions when food availability was low, the group sizes tend to be small.

Comparative studies to date lend support to this hypothesis. Elephants in the Serengeti form large herds in the wet season when food is plentiful and competition is presumably low. Elephant group sizes are also large on the periphery of population ranges where they come into conflict with the surrounding human population (Laws 1969b). In the Murchison Falls Park South the elephants living in the center of the park have a mean group size of 6.1, but those living on the periphery near human habitation have a mean group size of 22.5 (Laws, in press).

It has further been suggested that larger groups might occur in areas of high density because of the tendency of elephant group to keep together for a while after meeting, (ibid.) However the Manyara density is higher than the MFPS

Figure 6.31
Drought



During the Tsavo drought, the family units, fragmented of which these are typical examples.

(Photographs by courtesy of Simon Trevor)

high density stratum, but the mean group size of 9, from aerial counts is lower; therefore it seems that the human disturbance explanation of large elephant group sizes is more probable.

In contrast, under the conditions of Tsavo drought of 1971-72, when food availability became critical for individual survival, family units fragmented mainly into sub groups of three to five animals (Shedrick, 1972; S. Trevor, pers. Comm.; Fig. 6,31), and large groups were not observed.

The very slight increases in spacing and decreases in mean group size observed independently on the ground and from the air, in the dry season at Manyara, although not statistically significant are consistent with each other and may represent a slight tendency towards fragmentation and dispersal in periods of relatively scarce resources. However it is likely that competition resulting from seasonal variations in food availability is largely reduced by the permanent underground waters supplying the forests and swamps, and is not intense enough to cause dispersion.

In conclusion, during the study period at Manyara I never observed intraspecific aggressive behaviour or any other form of social stress which had any obvious adverse effect on the survival or reproduction of individuals, and on this evidence it is tempting to rule out any density dependent social factors as directly controlling population. Aggression arising from competition appeared to be the consequence of low resource availability rather than of density as such. In the next chapter the availability of these resources, the elephants use of them and elephant/ habitat interactions will be described.

CHAPTER 7 — ELEPHANT HABITAT INTERACTIONS

ELEPHANT HABITAT INTERACTIONS

Introduction

At the root of all elephant problems is their effect on the habitat. In areas with dense elephant populations, Woodlands and Forests have been almost completely destroyed beginning with the Murchison Falls Park (Buechner and Dawkins, 1961). This in turn has been correlated with a decline in elephant recruitment possibly due to malnutrition, or to heat stress, or both (Laws, 1970b; Field, 1971).

In order to collect more information on nutrition, I made systematic records of elephant feeding behaviour at Manyara. Their diet was further deduced from records of plants which showed obvious signs of recent elephant use. Out of the 650 species of trees, shrubs, herbs and grass growing within the Park boundaries (Greenway & Vesey-Fitzgerald, in prep.), the Manyara elephants fed on at least 134. These are listed in Appendix 9. Their preference for certain species and seasonal variations in diet will be published elsewhere, but it may be stated that there was no evidence of a shortage of browse or grazing at any time. This has been concluded independently by Vesey-Fitzgerald (in press), from a long-term study of vegetation plots distributed throughout the different habitats in the Park.

This does not mean however, that the food supply will remain sufficient in the future. I therefore paid special attention to possible long-term consequences of the elephant's feeding habits. As in many other areas, the most striking effect of elephants on their habitat was their destruction of mature trees woodland and forest types formed 50% of the Park area. The escarpment with many woody species occupied a further 26%, and pastures, swamps and glades in the forest occupied the remaining 24% of the Park, The woody habitats below the escarpment from North to South, and their percentage of the Park area were as follows:

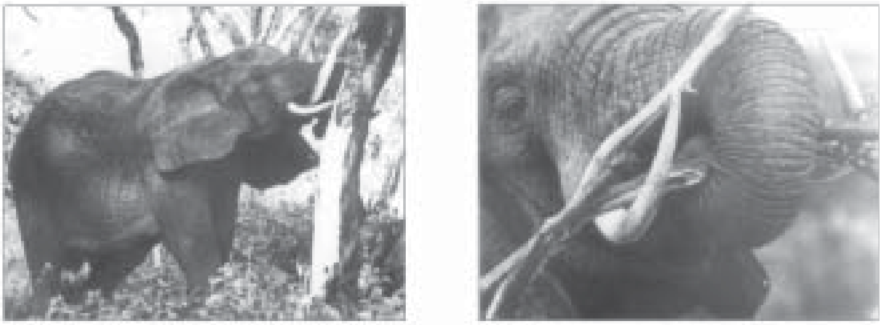
Northern	"Trichilea" Forest	17%
	"Acacia spp." Forest	8%
Central	Acacia tortilis woodland	10%
Southern	Mixed Woodland	15%

In 1966 the only obvious damage appeared in the *Acacia tortilis* woodlands. I often observed elephants gouging individual trees with their tusks and then pulling off large strips of bark with their trunks. The fibrous bark of the *A. tortilis* has a high tensile strength and tends to strip rather than break off in chunks. The damage and wound regeneration has been described by Savidge (1968). If more than half the bark has been removed the tree has little chance of surviving more than 4–5 years. Younger trees were

Figure 7.1

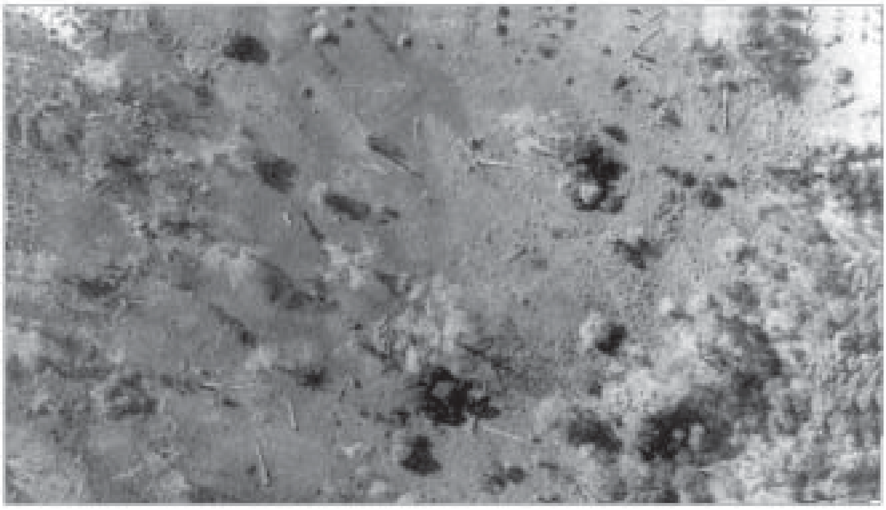
Elephants and trees: Lake Manyara National Park, 1970

A. Elephants in the rapidly declining *Acacia tortilis* woodlands.



B. Bark stripping of an *Acacia tortilis*.

C. The snapping of an *Acacia tortilis* sampling.



D. An example of elephants destruction in *Acacia xanthophloca* forest.

pushed over or their stems were snapped (Fig. 7.1 A-C). Feeding behaviour has been further described by Croze (1972). In assessing the extent of damage, I used a number of different methods.

Methods

In order to provide an overall estimate of species composition and the relative importance of elephant damage within each wooded habitat, the whole Park was sampled in late 1969 and 1970 by 25 semi-randomized, point centre quarter (P.C.Q.) transects (Cooper , 1963), Fig. 7.2 B. These were sited at random intervals in each habitat, and trees were sampled at regular points along each transect line in the following manner. At each point a wooden cross was set on the ground which divided the horizontal plane into four quadrants, always at a fixed angle to North. The nearest tree in each quadrant was identified, its distance from the cross and its diameter at human breast height (d.b.h.) was measured; and the degree of elephant damage was estimated, both for browse and for the amount of bark removed from each tree's circumference. The number of recording stations per transect ranged between 10 and 30, which was equivalent to 40 to 120 trees recorded on each.

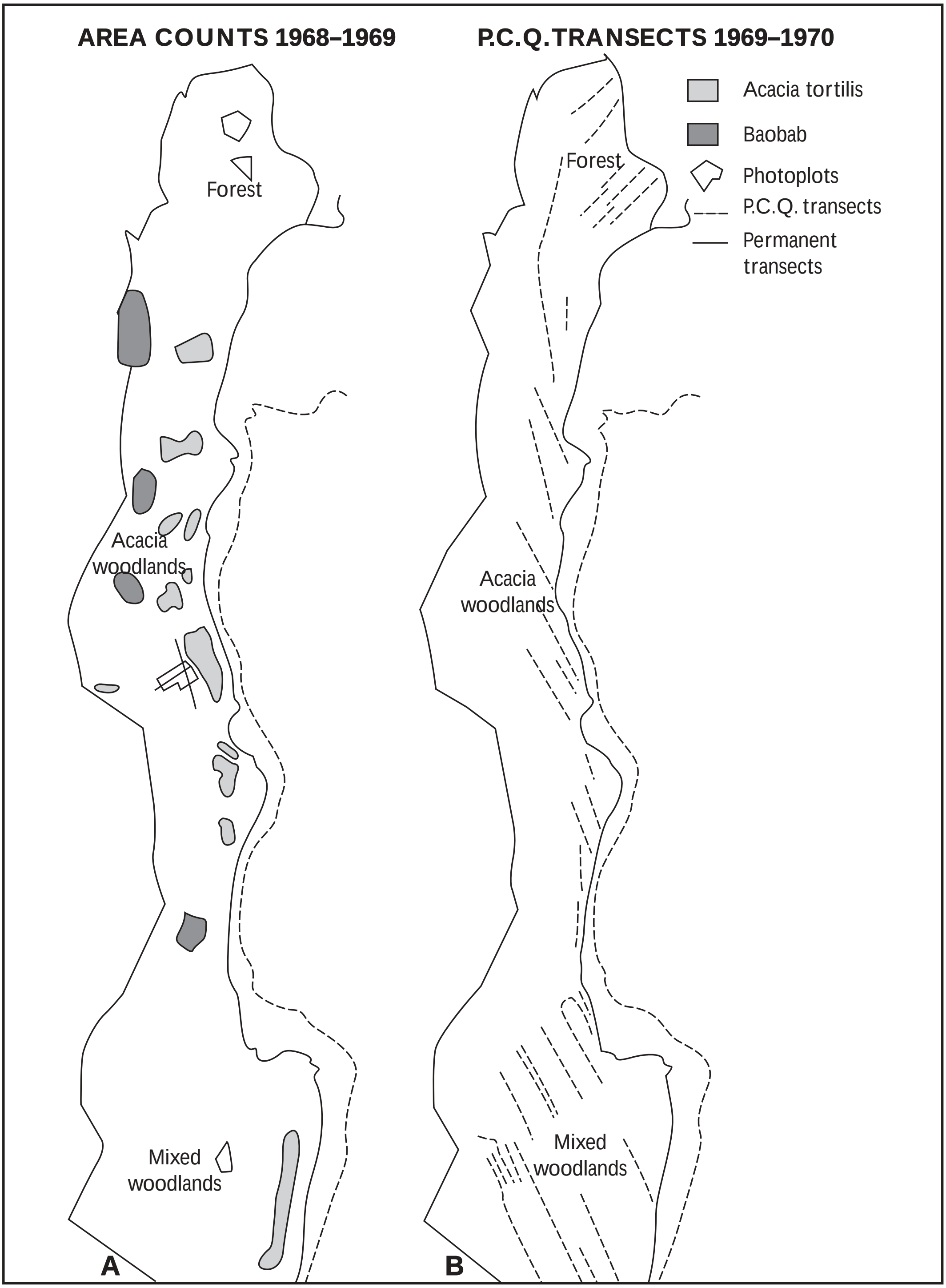
Long term changes in canopy cover in these habitats over 12 years were measured by comparing the earliest aerial photographs made in 1958 with later aerial photographs made in 1967 and 1970 as part of this study. All sets were enlarged to roughly the same scale, suitable plots were identified in each of the wooded habitats and exactly the same boundaries were marked around each plot by joining prominent trees with straight lines. Counts were then made of percentage canopy cover, using a perspex grid dot overlay.

The species Acacia tortilis (easily recognised on aerial photographs) was the subject of a special study. Its density, the size structure of 12 separate stands and elephant damage per size class, were obtained by area counts made in 1968, on the ground which totalled 4137 trees. Although these counts were not deliberately randomized in distribution (as they were chosen for ease of recognition on aerial photographs, so that they could be repeated in the future), they were widely scattered, and were representative of the woodlands (Fig. 7.2 A).

Unfortunately trees in the area counts were measured in circumference i.e. girth at breast height (g.b.h.), rather than the more widely used diameter at breast height (d.b.h.) which I later adopted in the P.C.Q. transects. This means that the results when compared are lumped in slightly different size classes.

The mortality and growth rates, of Acacia tortilis, and the timing and distribution of elephant attacks were also obtained from two fixed transects, with 355 numbered trees of this species. These were checked at frequent intervals.

Figure 7.2
Woodland and forest tree counts



Results (All Tables for Chapter 7 follow p. 177)

Unless a tree was pushed over or the trunk was snapped, browsing seldom caused fatal damage. The P.C.Q. transects which covered the whole Park in 1969 and 1970 showed that the amount of elephant damage varied greatly in the different wooded habitats depending on which was the dominant species.

I have pooled the data for each major wooded habitat, and have calculated the relative frequency of its component species. The results are summarized in Tables 7.1 – 7.6. The damage is tabulated for each of the commonest species. As browsing seldom fatally injured a tree the living trees were only categorized for bark damage.

Undamaged	The trunk intact with no injury from elephant tusks.
$< {}^{1}/_{2}$	The trunk gouged by tusks with anything from a small scrape mark to half the bark removed around the circumference.
$> {}^{1}/_{2}$	From half the bark removed around the trunk to almost all the bark removed.
Killed	The trunk totally debarked by elephants, or the tree killed by being pushed over or having its trunk snapped by elephants.
Dead	The tree dead either from a cause other than elephants, or so rotten that the cause of death could not be deduced.

In the Northern 'Trichilea' Forest the damage appeared slight. 48 per cent of the tall dominant 'Trichilea roka had trunks which had been gouged, but in most cases this was no more than a slight tusking, and not one had been killed or totally injured. The younger size classes of this species were less frequent than the older trees (Fig. 7.3 A), and those which were found were heavily browsed and it is possible that elephants were suppressing their regeneration, since of the 'browsers' elephants had by far the largest biomass. However mature stands of trees with almost closed canopies and virtually no regeneration of the dominant, are a feature of many tropical forests, even in the absence of elephants. The commonest trees in the understory were Conopharyngia usambarensis, Croton macrostachys, Rauvolfia caffra and Cordia goetzei, all of which showed little damage (Table 7.1) Two of the less common species, Acacia clavigera and Zanha Golun-gensis were damaged in each of the few specimens encountered, and it is possible that elephants may be eliminating certain highly favoured or particularly vulnerable species. However, a photoplot in this habitat of 0.2 Km^2 had a canopy cover value of 98 per cent both in 1958 and in 1970. It may be concluded that, as yet, 'Trichilea' forest has changed little, despite the high elephant density.

Figure 7.3 A
Elephant damage to Trichilea roka, the commonest forest species from P.C.Q. transects

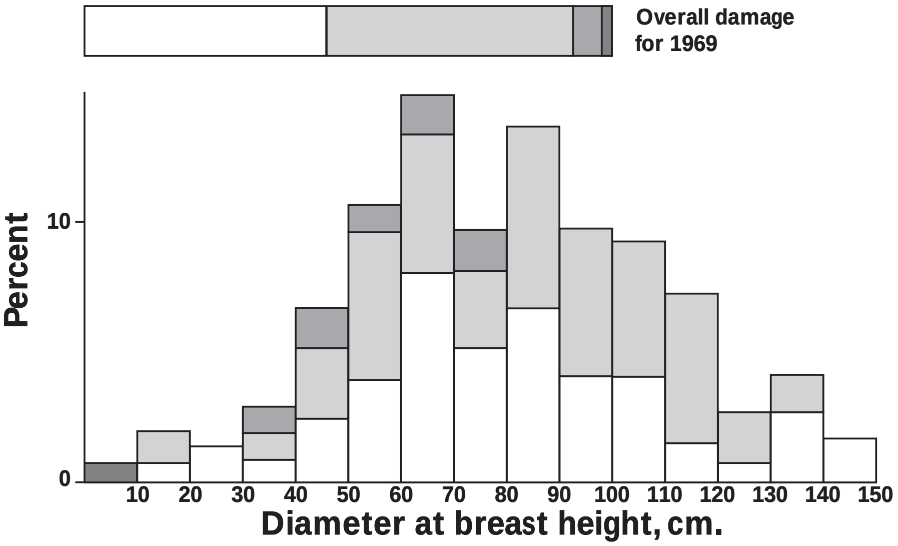


Figure 7.3 B
Elephant damage to Acacia tortilis, the commonest woodland species from P.C.Q. transects

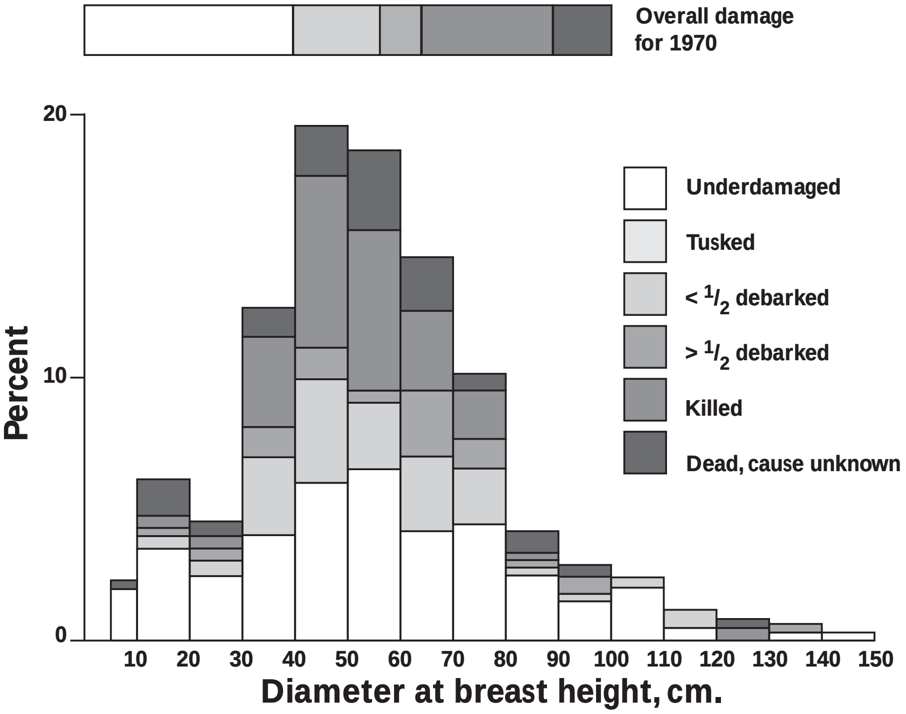


Figure 7.4 A
Elephant damage to baobab, Adansonia digitata.

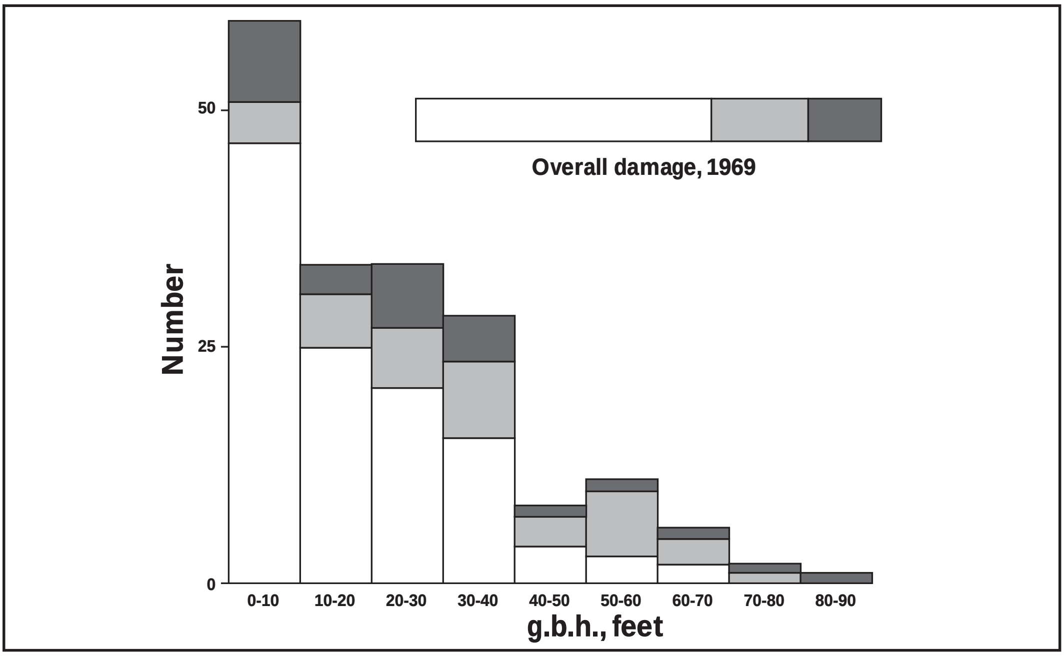
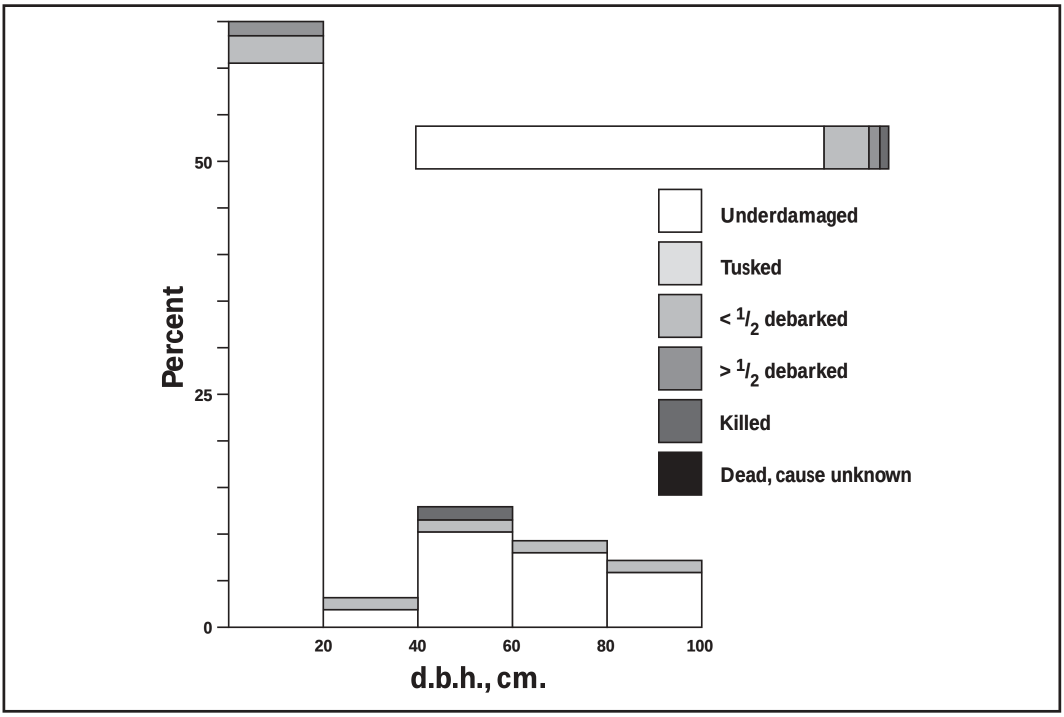


Figure 7.4 B
Elephant damage to Acacia sieberiana in mixed woodland, 1970.

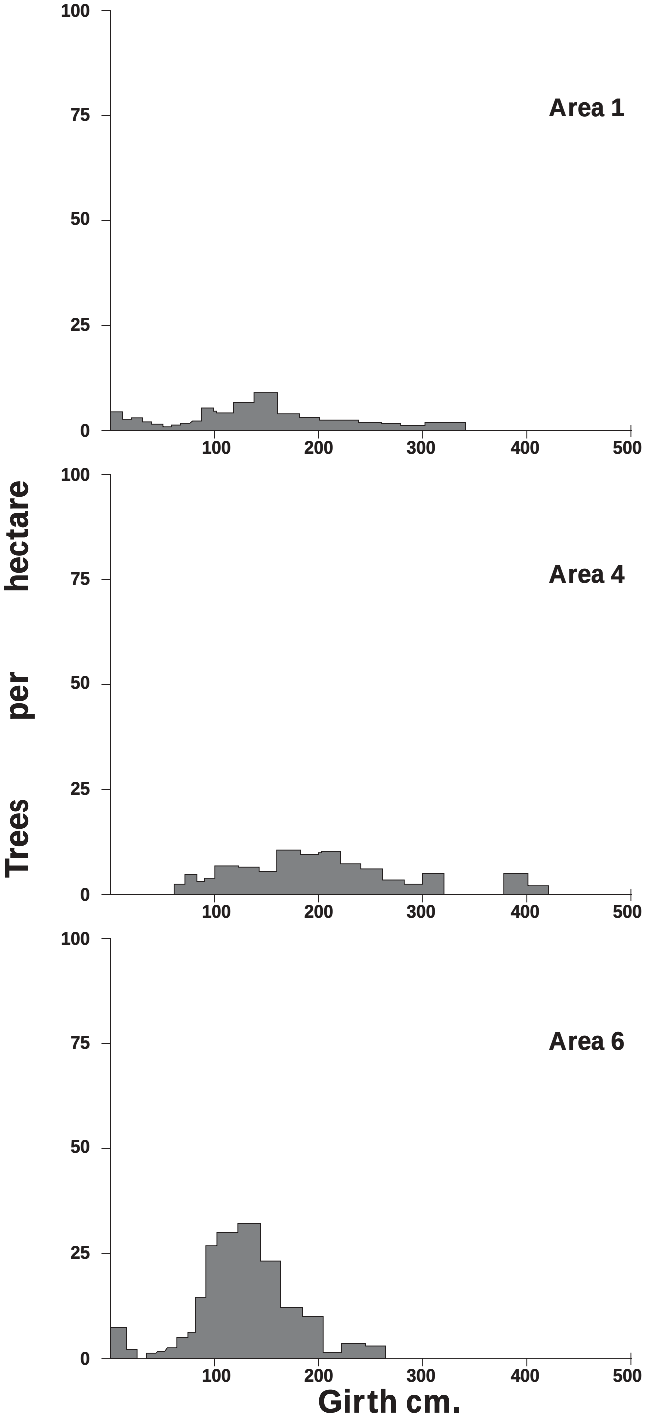


In the other type of northern forest, *Acacia* species were most common forming 54.1 per cent of the mature stands. Acacia xanthophloea, A. albida and A. tortilis showed severe signs of elephant damage. The most common tree, A. xanthophloea had been hardest hit, and only 28 per cent remained viable, the rest had been fatally stripped, killed or had been dead for some years (See Table 7.2). A photoplot in the 'Acacia' forest of 0.15 Km^2 had a canopy cover value of 34 per cent in 1958 which had been reduced to 21.3 per cent by 1970; a reduction of approximately one third over twelve years. Most of this habitat had become an open glade (Fig. 7.10 D). It is relevant to note that the Makerere University expedition of 1961 to Manyara remarked on the decline of Acacia xanthophloea in this habitat, but observed, that the bark on most trees was intact being little touched by elephants. The large quantities of dying trees then observed, they suggested, might have been caused by streams shifting in flood periods, perhaps leaving the trees stranded in soils with a much too low water content for part of the year (Typescript expedition report). Perhaps therefore these trees were time expired even before the current high level of bark stripping. In some of the glades within and around the Northern forest, Acacia xanthophloea showed vigorous regeneration despite heavy browsing pressure. This species grows fast and Mr. J. Hopcroft informed me that he measured individual specimens which had grown to a diameter of 60 cm in 40 years at Lake Naivasha. It is possible that within 20-30 years some of the forest glades at Manyara may become A. xanthophloea forest.

The Acacia tortilis woodlands further South were in rapid decline. Acacia tortilis, the dominant tree, formed 84 per cent of the stands and was severely damaged (Table 7.3). Only 54 per cent of the trees of this species were found alive with enough bark left around their trunks to remain viable (i.e. < $^1/_2$- remained) Fig. 7.3B summarizes the frequency of A. tortilis size classes and relative damage in 1970. The potential regeneration is not indicated on this histogram, as in the P.C.Q. transects no trees were measured of less than 5 cm d.b.h. However the size structure shows that there were too few trees between 5 and 30 cm. d.b.h. (16 and 94 cms g.b.h.) to replace the old trees in the larger size classes if these should be destroyed. The second commonest tree in this woodland type, Balanites aegyptiaca, was very little damaged by elephants. Above 93 per cent were viable and none were found which had obviously been killed by elephants. A photoplot of 0.42 Km^2 showed canopy cover values of 31.2 per cent in 1958, 26.9 per cent in September 1967 and 23.6 per cent in March 1970. More precise mortality rates of A. tortilis are discussed later.

In the South of the Park were the mixed woodlands, and transect results have been pooled in three separate categories. North of the River Endabash, five short transects were made in one small area of fire induced park land in which mature Balanites aegyptiaca and regenerating A. sieberiana were common. This sub-area showed little signs of elephant damage and more than 90 per cent of both species were viable (Table 7.4).

Figure 7.5
Acacia tortilis size structure and density mature stands



In the rest of the Southern mixed woodland, slight differences in the frequency of species were found North and South of the Endabash River, but the commonest trees in both areas were: *Acacia sieberiana*, *Croton macrostachys*, *Balanites aegyptiaca*, *Gardenia jovistonantis* and *Zizyphus pubescens*. None of these species showed serious signs of elephant damage, and *Gardenia* by virtue of its dense canopy descending to ground level and surrounding the stem appeared virtually immune to debarking (Tables 7.5 and 7.6). A photoplot in this area of 1.5 Km^2 had a canopy value of 24.1 per cent in 1958 and 21.6 per cent in 1970, an insignificant decrease. *Acacia sieberiana* was attacked much less than other species of large *Acacia* with > 85 per cent undamaged, and young size classes were found in abundance, indicating a healthy recruitment (Fig. 7.4A). It is relevant to note that Field (1971) has recorded a high incidence of bark damage to this species in the Queen Elizabeth Park with only 7 per cent undamaged by elephants.

Thus in the four major wooded habitat types, the P.C.Q. transects and photoplots showed that in 1970 only the *'Acacia'* forest and the *A. tortilis* woodlands had declined since 1958. The escarpment was not assessed by transects but special counts were made in 1969 of baobabs, *Adansonia digitata* which grew in profusion on its slopes. In contrast to almost every other area where elephants at high density occur together with baobabs, these huge trees suffered little damage at Manyara. 64% were undamaged and none were seriously attacked or destroyed (cf. Savidge, 1968; Laws, 1970b). Younger trees were more frequent than older trees and this habitat provides an example of regeneration in this exceptionally long-lived species (Fig. 7.4 A).

In previous years a special study was made of the *Acacia tortilis*. In 1968, twelve total counts in separate areas showed that the *A. tortilis* tended to grow in even-aged stands. The area counts fell into two types, those which contained exclusively mature trees and those in which regeneration predominated. Examples are given in Fig. 7.5 and 7.6 where size classes have been plotted in density frequency histograms. Virtually no young *A. tortilis* were found growing under the mature trees and were probably inhibited from by too much shade or even perhaps by some root exudate from adults. Young *A. tortilis* did germinate under the adults, but they did not survive.

When the results of all area counts are pooled, the size frequency distribution is very similar to the P.C.Q. results and shows a bimodal distribution centering around 0–10 and 120–140 cm g.b,h. (0–3 and 38–45 cm d.b.h.).

There are very few trees in the 20–100 cm g.h.h. (6–32 cm d.b.h.) size classes (See Fig. 7.7 A). The smallest size classes up to 30 cm. d.b.h. are little damaged on their stems (Fig. 7.7 B), because at this age the *A. tortilis* is a well protected thorny shrub with little stem exposed. As the tree grows taller it becomes easier for the elephants to find a gap in the defences. Buffalos also frequently damage the bush by rubbing against the saplings with the bosses of

Figure 7.6
Acacia tortilis size structure and density regenerating stands

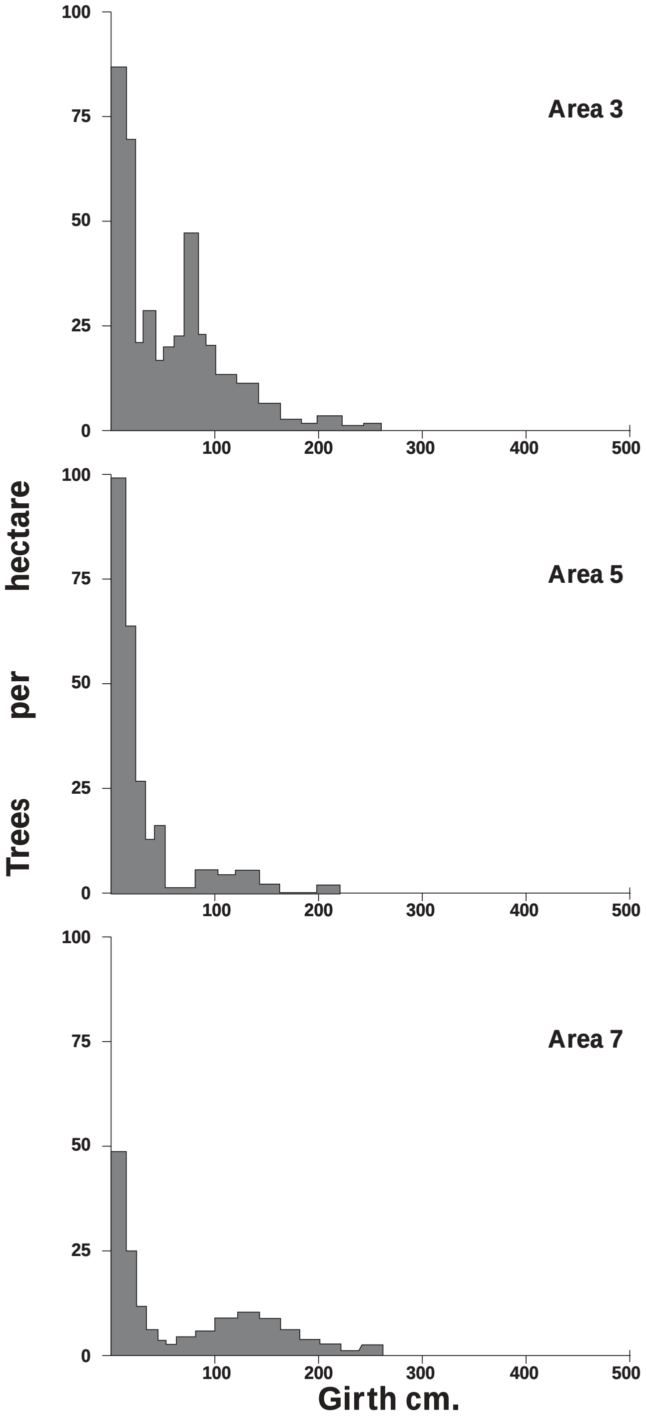


Figure 7.7 A
Acacia tortilis size classes from combined area counts of 1968

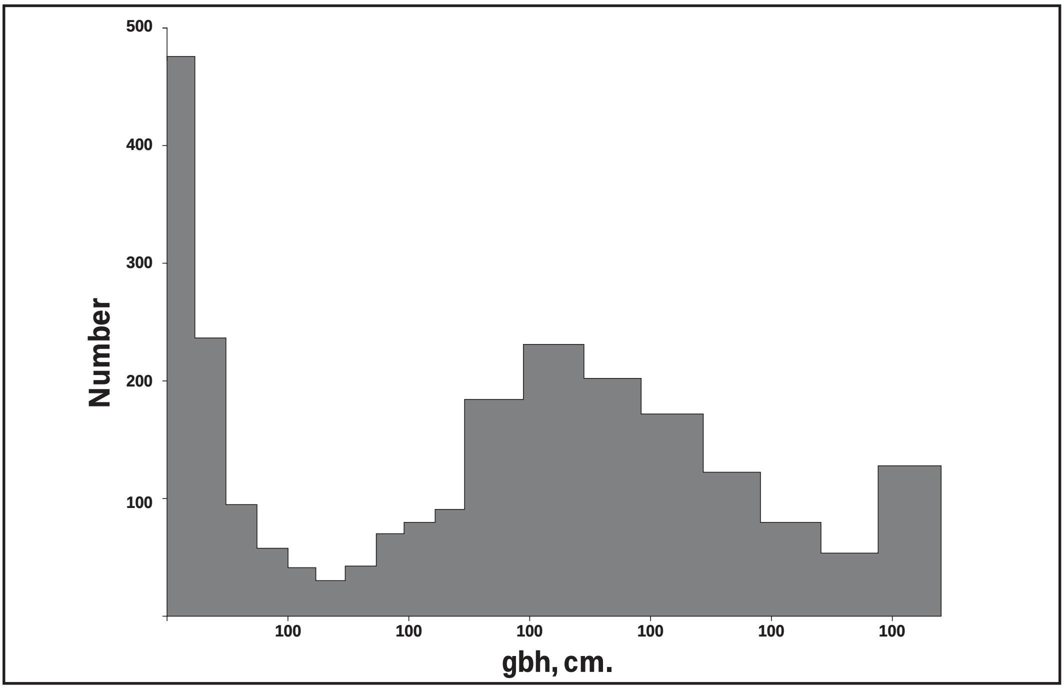
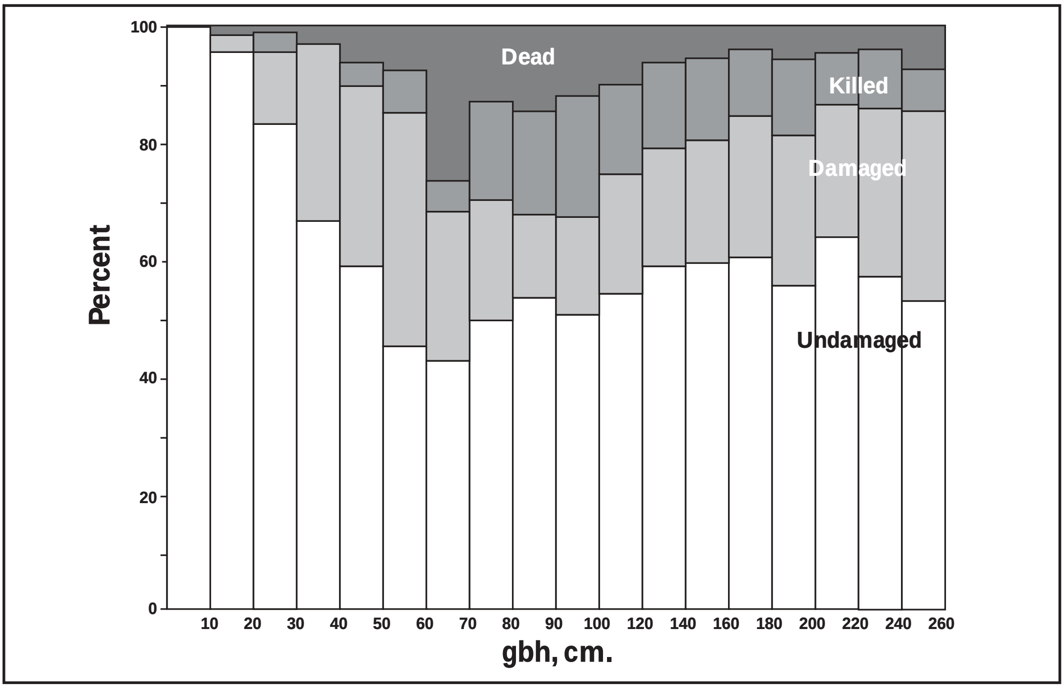


Figure 7.7 B
Frequency of elephant damage to Acacia tortilis per size class



their horns and impala are avid browsers on young A. tortilis. The 50-80 cm g.b.h. sizes showed the heaviest bark damage and appeared to be particularly vulnerable to stripping, snapping and pushing over, which may largely account for their relative infrequency. Although the regeneration potential existed, there seemed to be a dangerous period through which the trees had to pass before reaching maturity. However even the mature trees were not surviving well during the study period.

The results of the twelve area counts made in 1968 in the Acacia tortilis woodlands can be compared with the results of the ten P.C.Q. transects made in 1970. The mean percentage of trees alive in 1968 was 82 per cent which had declined to 64 per cent in 1970, a mean annual mortality of about 9 per cent (Tables 7.7 A and 7.7 B). As the area counts were not truly random samples, confidence limits on the means are not given. However the samples were large and widely distributed and the difference between these means, is probably representative of the overall decline of this species within the Park. If this estimated trend remains constant, almost all mature Acacia tortilis will be dead by 1980.

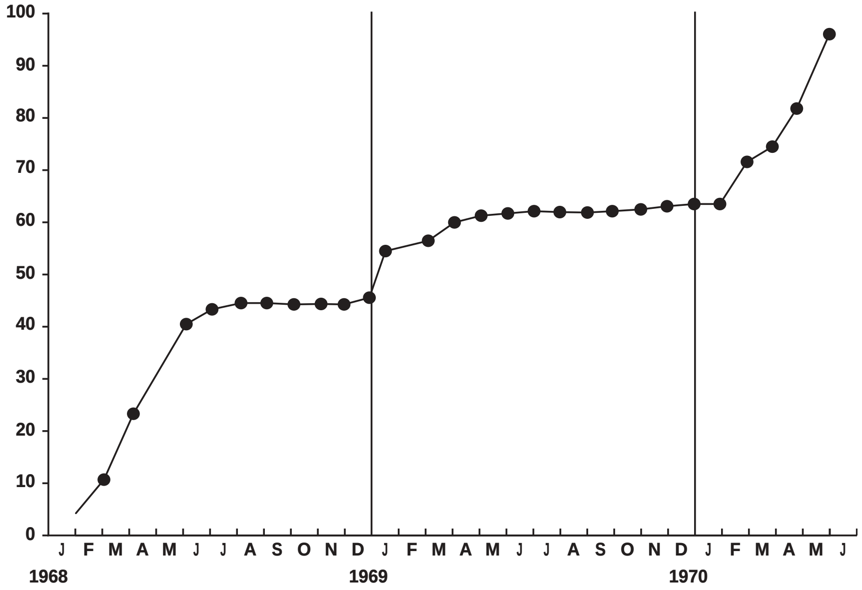
More precise mortality data in the Ndala area were obtained from two fixed transects. These showed that elephant attacks were concentrated in the rainy season. In Fig. 7.8 A & B, cumulative rainfall and cumulative attacks by elephants on the two transects are adjusted to the same percentage scale. In both 1968 and 1969, bark stripping began just before the end of the dry season i.e. at a time when these trees came into leaf. Stripping continued throughout the rainy season but declined almost completely as the Park dried up from June until November.

Of the 92 trees that died, 81 were killed by elephants and the remainder died of unknown causes. The survivorship on these two transects is illustrated in Fig. 7.9. The pooled results give a mean annual mortality of 11.7 per cent of the original stand. If present trends continue, there will be no trees alive on transect 1 by 1982, and on transect 2 by 1976.

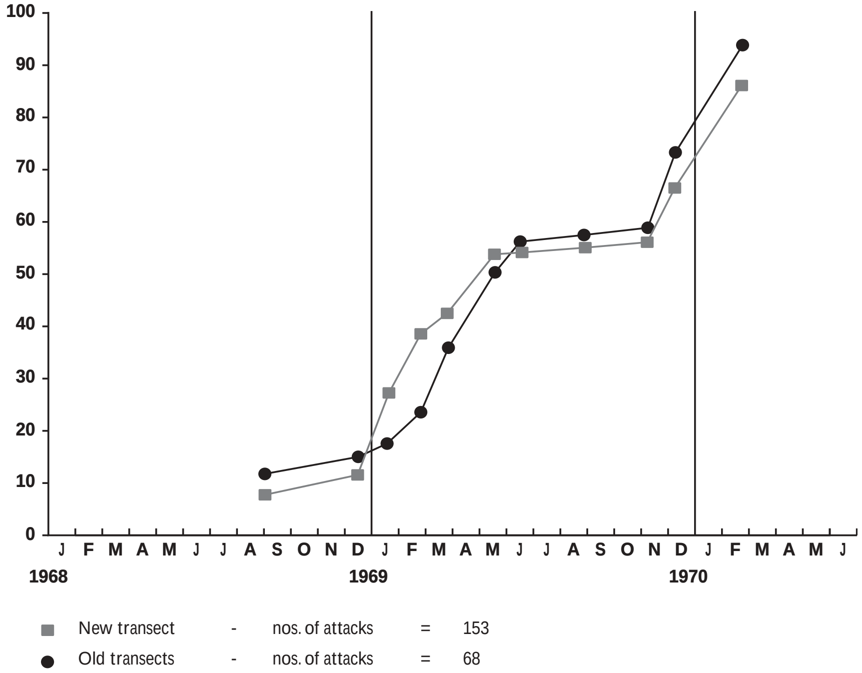
The fixed transect records also indicate that younger age classes suffered a higher mortality rate than the older ones. However elephants did not appear to attack these younger trees more than others. As Table 7.8 indicates, the frequency of elephant attacks per individual tree showed no trend related to size class. Although the percentage annual mortality dropped off with increasing size, the mean number of attacks per tree remained relatively constant on both transects. On average, elephants took a fixed amount of bark ‘in each attack, and the younger trees, having a smaller circumference, obviously had a larger proportion of it removed which probably accounts for their greater mortality. This may explain why in the area counts and P.C.Q. transects, the age classes between 20 and 100 cm g.b.h. formed such a small proportion of the population. In contrast, the old trees were often gnarled and elephants seemed to have difficulty in prizing off bark with their

Figure 7.8
Elephant attacks on 221 A. tortilis trees in relation to rainfall

A. Cumulative % Rainfall - Ndala Guage.



B. Cumulative % attacks by elephants on Acacia tortilis.



tusks. The constancy of mean attacks per tree also contradicts any suggestion that elephants tend to select senile trees.

In view of the imminent destruction of the Acacia tortilis woodland, it was relevant to study the growth rate of this species in order to estimate the time needed before new stands could arrive at maturity. Growth in circumference was measured for 61 undamaged A. tortilis trees, over periods of one to two years. As the bark was very corrugated, the measurements needed to be taken at precisely the same level each time. This level was marked by small nails, and the circumference measured by a steel tape drawn tightly around the tree.

The results are summarized in Fig. 7.10. Growth rates show great individual variation. Means are calculated for 50 cm g.b.h. classes and 95 per cent confidence limits on each mean are indicated, except where the sample size was less than 5. The mean growth rate of smaller trees is obviously faster than the older trees and it is likely that the growth rate in these even-aged stands gradually slows down throughout the life of an individual as its crown comes into competition with others and eventually stops altogether. However, even the largest trees in the Manyara sample were still growing and circumference growth obviously continued for longer than vertical growth. Variation in the individual rates was probably caused by edaphic factors, rainfall and the density of trees within the stand. A curve has been fitted to these means by eye. A straight regression line could have been used but growth rates are unlikely to decline in a linear manner, and even the largest trees still showed some growth. Although my method is approximate, the growth measurements are so scattered that this curve is adequate for the purposes of constructing an approximate mean girth at age key.

The mean girth at age (Fig. 7.11) was obtained by calculating the cumulative time taken for a tree to grow through each of the size classes at the average age-specific growth rate. This ageing key is based on assumptions which may have to be modified after the collection of further data. Firstly the growth rates were possibly high since they were measured over a short period during which the rains were favourable, and mean annual growth rates of trees are extremely variable in the tropics (Dr. H.C. Dawkins, pers. comm.). Secondly they were taken only from trees in the Ndala area of the Park, and other areas might show considerable differences in mean growth rate. With these provisos in mind, an attempt to estimate the mean age of a stand of A. tortilis can only be a first approximation, but even the slowest rates of growth indicated by the lower 95 per cent limit curve in Fig. 7.10 suggest that this species grow relatively fast.

When the age size key is applied to the overall size distribution of the Acacia tortilis population, it indicates that the mode at 120-140 cm g.b.h. corresponds to a mean age of 30 years. It is probably safe to predict that if elephants were to completely destroy These woodlands in the near future, it would take at least another 50 years before a comparable

Figure 7.9
% *Acacia tortilis* alive on transect 1 and 2

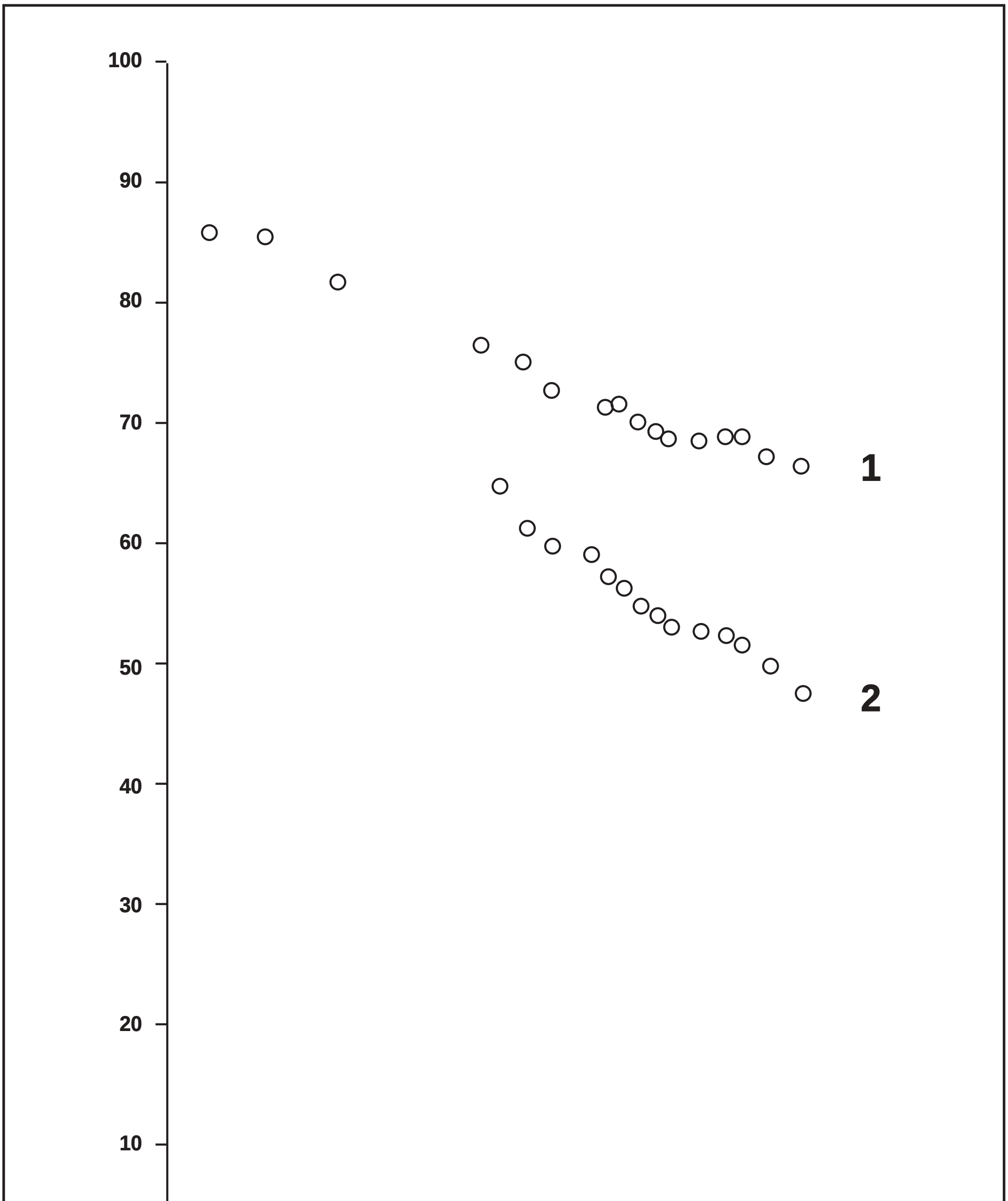


Figure 7.10
Mean annual growth in circumference of *Acacia tortilis*

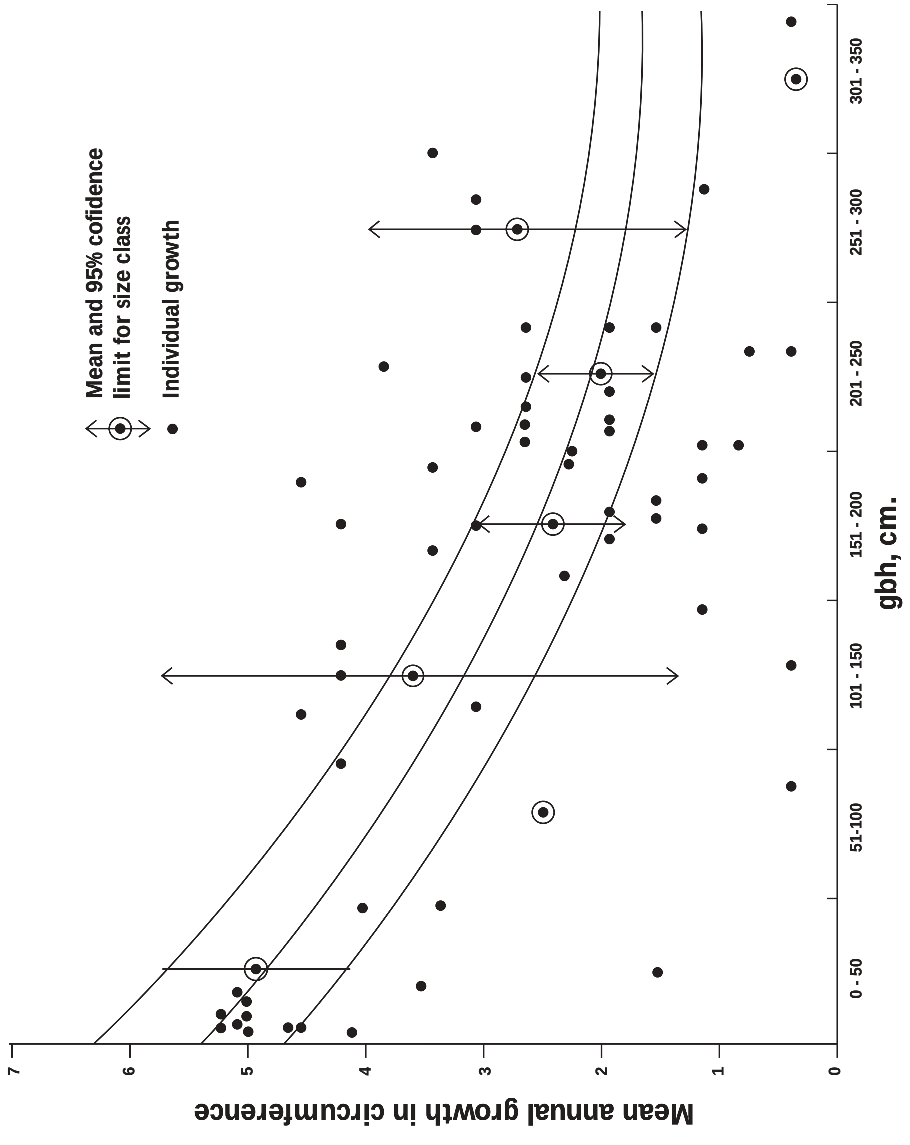
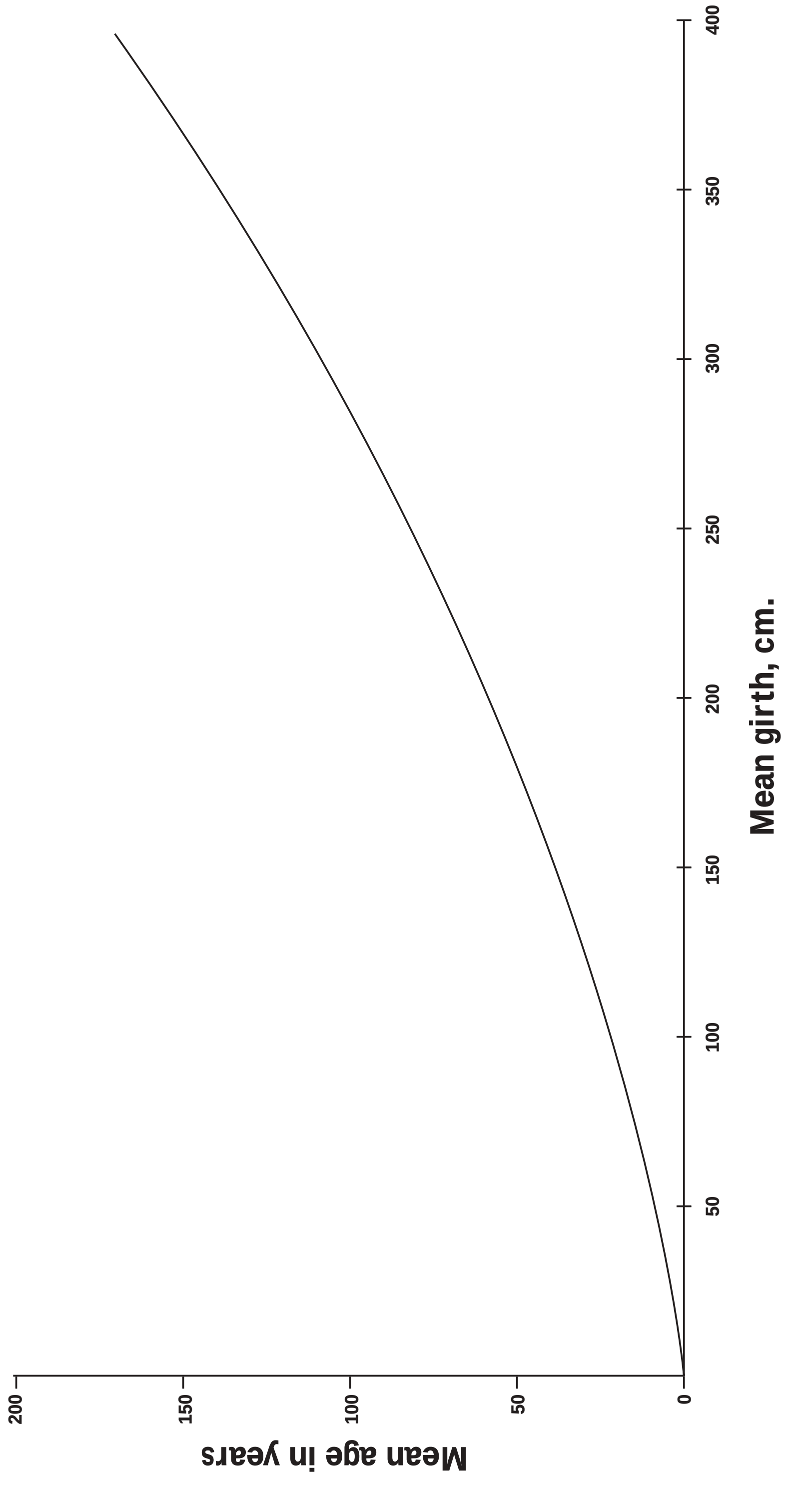


Figure 7.11
Acacial tortilis age/circumference key



stand could be established in this area and then only if the regeneration potential were unsuppressed by browsing animals. It is hoped to obtain more reliable age estimates, from five years of data, by repeating these measurements in 1973.

Even after the mature stands have been eradicated, A. tortilis seedlings are still likely to be widely distributed since this species depends on animals for dispersal. The seed pods are aromatic, and it has been suggested by Lamprey (1967) that they have evolved their convoluted shape so that they can be easily picked up by the animals which feed on them. Experiments have shown that the passage through the gut of a mammal facilitates germination and protects the seeds from their major bruchid parasites (Lamprey, pers. comm.). Elephants, impala and baboons all feed on these pods. It has been observed that during the fruiting season, bull elephants shake the trees to dislodge large quantities of pods, which are rich in carbohydrates and proteins, and form a conspicuous and easily available food source in the dry season both for the bulls and for the family units which follow the bulls around in order to participate in the feast. Extensive germination experiments were made on A. tortilis seeds, as part of this study, which will be published elsewhere. Over 100 seeds were counted in one bolus, and elephant ingested seeds had a high germination success of the order of 10 - 20 per cent. I often encountered elephant dung with numerous Acacia seedlings sprouting from each bolus (Fig. 7.12 B). Unfortunately, this positive effect of elephants which increases the regeneration potential does not counteract the excessive mortality inflicted on the older age classes above 30 cm g.b.h. (10 cm d.b.h.).

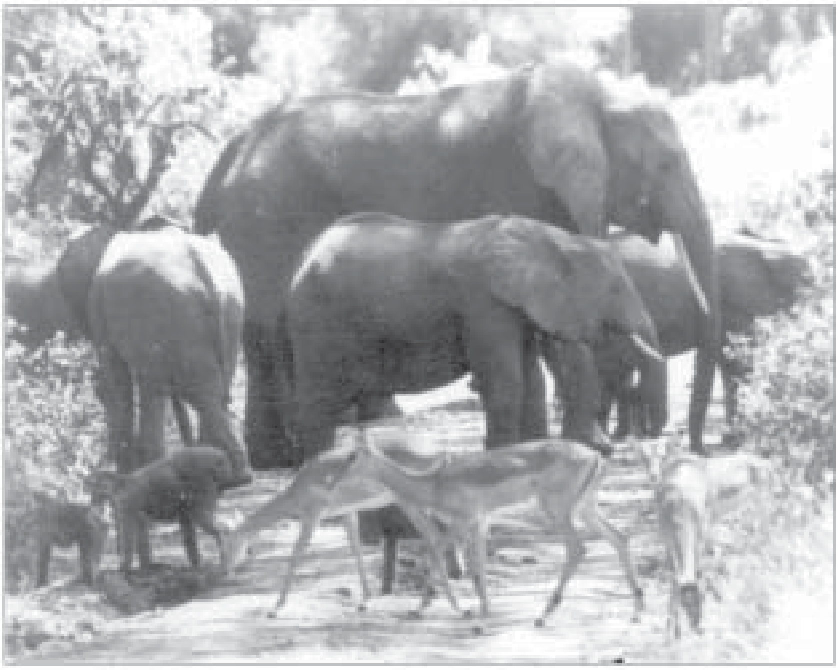
Discussion

In previous years no observations were made in Manyara suggesting that the elephants caused serious damage to woody species, despite qualitative surveys by experienced observers (Morgan-Davies, Iain D.H., 1968–1963; Van Rensburg, 1961; Kinoti, 1961; Greenway and Vesey-Fitzgerald, 1969). Even Watson and Turner (1965), who suggested that the Park might be over-populated with elephants, remarked “there are no signs of excessive damage to trees.” It seems therefore that serious tree damage began only shortly before the study period, and it is tempting to conclude that it was caused by the driving of the Magara elephants into the Park. The situation probably has been aggravated by the loss of extensive swamps in 1968, which were formerly a favoured elephant habitat but which are now submerged under the Lake. There is also a possibility that changes in mineral concentration within the bark, associated with the rise in the water table, might somehow affect the rate of elephant attacks, as suggested by D. Western (pers. comm.) for Acacia sp. in the Lake Amboseli area of Kenya.

The Manyara eco-system conforms to the familiar pattern seen elsewhere, with overpopulated elephants destroying woodland faster than it can regenerate, but it must be stressed that at present only

Figure 7.12

The dispersal and germination of Acacia tortilis.



A. Elephants, impala and baboons feeding on Acacia tortilis ***pods.***

B. Acacia tortilis seedlings sprouting from a heap of elephant dung.

one woodland type is being eliminated. It is possible that when the present cycle of wet years is finished and the A. tortilis woodlands have been destroyed, the elephants will turn to other species and start eliminating the forests but time remains to continue monitoring for several more years before 'irreversible' changes have been made. The almost total eradication of woodlands and forests, by elephants at a lower density than at Manyara in the Murchison Falls, Queen Elizabeth and Tsavo National Parks, suggests that this might also happen in Manyara. Fire prevented regeneration in these areas, and although this factor is absent in Manyara, regeneration appears to be suppressed by animals alone. If the Park becomes completely deforested, it is unlikely to be suitable habitat for elephants. However, the destruction is at an early stage, and if the loss of the A. tortilis woodlands is acceptable, there are still some years before the 'Trichilea' forest and mixed woodlands will be endangered.

Therefore I conclude that, even though the Manyara population of elephants does reduce A. tortilis more rapidly than this species regenerates, there is as yet no reason to start culling elephants although this course of action should not be ruled out in the future should all other approaches fail. At present, the area should be used for continued long-term studies now that a base line has been established.

Table 7.1

F.C.Q. Transect counts: ‘Trichilea’ forest, 1969.

Species	No.	% Relative Frequency	% Undamaged	% Bark removed		% Killed	% Dead
				$<{}^1/_2$	${}^1/_2>$		
Trichilea roka	125	28.2	46	53	0	0	1
Conopharyngia usamberensis	75	16.9	43	46	1	0	10
Croton macrostachys	67	15.1	45	50	2	3	0
Rauvolfia caffra	48	10.8	38	58	0	0	4
Cordia goetzei	43	9.7	45	39	2	2	12
Acacia xanthoploea	18	4.1	11	17	11	55	3
A. clavigera	12	2.7	0	17	25	50	8
A. sieberiana	10	2.2					
Ficus sycamorus	9	2.0					
Phoenix reclinata	8	1.8					
Zanha golungensis	7	1.5					
Antiaris toxicaria	3	0.7					
Ekebergia buchananii	3	0.7					
Balanites aegyptiaca	2	0.4					
Bridelia micrantha	2	0.4					
Celtis zenkeri	2	0.4					
Acacia tortilis	1	0.2					
Celtis africana	1	0.2					
Cordia africana	1	0.2					
Kigelia africana	5	1.1					
Total	**443**						

Table 7.2

F.C.Q. Transect counts: ‘Acacia’ forest, 1969.

Species	No.	% Relative Frequency	% Undamaged	% Bark removed		% Killed	% Dead
				< $^1/_2$	> $^1/_2$		
Acacia xanthophloea	54	31.2	6	22	10	55	8
Cordia goetzei	27	15.6	41	59	0	0	0
Conopharyngia usamberensis	24	13.8	63	25	0	8	4
Acacia albida	19	10.9	0	66	10	14	10
A. tortilis	14	8.0	22	57	0	21	0
Trichilea emetica	11	6.4	9	82	9	0	0
Acacia sieberiana	7	4.0					
Rauvolfia caffra	4	2.3					
Hyphaenae sp.	3	1.5					
Kigelia africana	3	1.5					
Phoenix reclinata	3	1.5					
Celtis zenkeri	1	0.5					
Croton macrostachys	1	0.5					
Ficus sycamorus	2	1.0					
Total	**173**						

Table 7.3

P.C.Q. Transect counts: '<u>Acacia tortilis</u>' woodland 1970.

Species	No.	% Relative Frequency	% Undamaged	% Bark removed		% Killed	% Dead
				< $^1/_2$	> $^1/_2$		
Acacia tortilis	452	76.1	38	16	10	21	14
Balanites aegyptiaca	59	9.9	89	4	2	0	5
Gardenia jovistonantis	26	4.3	100	0	0	0	0
Ziziphus pubescens	16	2.6	88	7	6	0	0
A. sieberiana	10	1.6	90	10	0	0	0
Connopharyngia usamberensis	9	1.5					
Kigelia africana	8	1.3					
A. clavigera	3	0.5					
A. mellifera	2	0.3					
A. xanthophloea	2	0.3					
Ficus sycamorus	2	0.3					
Rauvolfia caffra	2	0.3					
A. albida	1	0.15					
Conniphora	1	0.15					
Cordia goetzei	1	0.15					
Total	**594**						

Table 7.4

P.C.Q. Transect counts: Mixed woodlands (Southern), 1970.

TRANSECT 1–5

Species	No.	% Relative Frequency	% Undamaged	% Bark removed $<{}^1/_2$	% Bark removed $>{}^1/_2$	% Killed	% Dead
Acacia sieberiana	88	66.6	76	21.5	2.5	0	0
Balanites aegyptiaca	40	30.3	72	18	5	2.5	2.5
Ziziphus pubescens	3	2.2					
Kigelia africana	1	0.8					
Total	**132**						

Table 7.5

F.C.Q. Transect counts: Mixed woodlands, 1970.

TRANSECTS 6–10

Species	No.	% Relative Frequency	% Undamaged	% Bark removed $<{}^1/_2$	% Bark removed $>{}^1/_2$	% Killed	% Dead
Balanitus aegyptiaca	127	38.2	86	5	4	0	5
Ziziphus pubescens	125	37.6	85	11	3	0	1
Acacia sieberiana	40	12.0	93	5	2	0	0
Croton macrostachys	26	7.8	83	17	0	0	0
Kigelia africana	5	1.5					
A. tortilis	4	1.2					
Gardenia jovistonantis	3	0.9					
A. clavigera	1	0.3					
Terminalia sp.	1	0.3					
Total	**332**						

Table 7.6

P.C.Q. Transect counts: Mixed woodlands 1970.

TRANSECTS 11–15

Species	No.	% Relative Frequency	% Undamaged	% Bark removed		% Killed	% Dead
				$<{}^{1}/_{2}$	$>{}^{1}/_{2}$		
Ziziphus pubescens	181	51.9	91	6	2	0	1
Acacia sieberiana	53	15.1	87	7	0	2	4
Balanites aegyptiaca	48	14	94	4	2	0	0
Gardenia jovistonantis	29	8.3	100	0	0	0	0
Croton macrostachys	11	3.1	82	18	0	0	0
A. tortilis	6	1.7					
Kigelia africana	6	1.7					
Trichilea eametica	5	1.4					
A. albida	3	0.8					
Cordia goetzei	3	0.8					
Ekebergia buchananii	3	0.8					
Ficus sycamorus	1	0.2					
Total	**349**						

Table 7.7A

Area Counts (blocks 1–12) of Acacia tortilis woodlands, 1968.

Block No.	No.	% undamaged	% Bark damaged	% killed	% dead
1	363	51	23	17	9
2	409	48	21	25	8
3	248	67	28	3	3
4	166	72	14	12	2
5	179	89	5	3	4
6	824	65	16	7	12
7	1,123	76	15	5	4
8	211	71	19	4	5
9–10	204	51	27	5	16
11	446	47	27	17	9
12	166	63	5	4	27
total mean%	**4,339**				
		64	**18**	**9**	**9**
		mean % alive	82		

Table 7.7B

P.C.Q. Counts (transects 16–25) of Acacia tortilis woodlands, 1970.

Block No.	No.	% undamaged	% Bark damaged		% killed	% dead
			<0.5	>0.5		
16	102	41	20	16	19	5
17	58	43	7	3	10	36
18	72	24	24	8	32	13
19	74	42	18	12	18	11
20	38	32	0	26	29	13
21	17	30	24	0	24	24
22	22	45	18	0	18	18
23	28	61	7	0	18	14
24	30	47	23	7	13	10
25	11	18	18	27	36	0
Total mean%	**452**					
		38	**16**	**10**		
			mean % alive	64		

Table 7.8

Mortality of Acacia tortilis per size, class and mean attacks per tree.

	g.b.h classes, cm.					
	50–60	**100–150**	**150–200**	**200–250**	**250–300**	**over 300**
Transect total Apr. 68-May 70	62	75	70	19	13	10
Mean annual mortality, %	25	11	9	10	8	3
Transect total Apr. 66-May 70	10	21	30	35	7	2
Mean annual mortality, %	15	5	5	4	4	0
Mean attacks per tree	1.2	1.17	1,16	1.84	1.20	1.29

Note that while mean annual mortality decreased with increasing size on both transects, the mean attacks per tree remained relatively constant.

CHAPTER 8 — POPULATION DYNAMICS

POPULATION DYNAMICS

Introduction

In the preceding chapters it has been demonstrated that despite the exceptionally high density of elephants that existed at Manyara, there was no behavioural evidence suggesting social "stress". The high density of elephants did however appear to be causing habitat changes. In places the Acacia tortilis woodlands were disappearing rapidly and this was directly caused by the feeding behaviour of the elephants. However, by August 1970 there was neither obvious deficiency in food for the elephants, nor insufficient shade due to lack of canopy cover. There was no evidence that nutritional stress, heat stress, or some behavioural mechanism (Laws & Parker, 1968) decreased individual reproduction during the study period. The overall population trends may be summarized by calculating the fertility, mortality and age structure of the population, which can be registered in a random sample of the population.

Comparative information on the status of other populations comes mainly from the work of Laws (1966, 1969a,b, 1970, in press), Laws & Parker (1968), Laws et. al. (1970), Hanks (1969, 1972). These populations were situated in areas which are abbreviated as follows:

Uganda	Murchison Falls Park North	- M.F.P.N.
	Murchison Falls Park South	- M.F.P.S.
	Budongo Forest Central Reserve	- B.F.C.R.
	Queen Elizabeth National Park	- Q.E.P.
Kenya:	Tsavo National Park	- T.N.P.
Tanzania:	Mkomazi Game Reserve	- MK.
Zambia:	Luangwa Valley	- Luangwa

Objectives

1. The estimation of fertility, mortality and age structure of the Manyara population for comparison with other populations.

2. The prediction of future trends in population size.

Fertility

Recruitment is dependent on the rate at which females reproduce and the proportion of females in the population which are in reproductive condition. The fertility of an individual female usually varies with age, and each age class has its age specific fertility. With small samples, such as those obtained at Manyara, only a mean birth rate can be calculated, usually expressed as a mean calving interval. The number of reproductive females depends on the age at which females attain puberty, and the age of menopause at which they stop reproducing.

Birth Rate and Calving Interval

Many workers in other areas have considered the annual birth rate to be one of the most important factors to estimate, as an index of the demographical status of an elephant population (Buechner et al. 1963; Bass & Savidge, 1966; Laws, 1966; Dodds & Patton, 1969; Field, 1971). Commonly the ratio of animals in their first year to the rest of the population has been used as a measure of the birth rate for that year. Unfortunately, both the annual birth rate and this method of calculating, are liable to give misleading results when dealing with elephants.

Firstly, it is difficult to decide the borderline between a first year calf and one which has entered its second year. A rough rule of thumb originally proposed by Buechner et. al. (1963) and supported by Laws (1966) is that first years may be recognised as those which can pass under the front legs of their mothers. While my own observations on calves, whose birth date is known to the nearest months confirm that this is approximately true, in the absence of a marked calving season at Manyara there is no sharp difference between the calves of one year and the calves of the next. Any slight subjective bias towards the inclusion or exclusion of calves on the borderline would greatly distort the estimated birth rate.

A second error is caused by the variations in first year mortality from year to year. This variation is pronounced in areas with marked climatic fluctuations, e.g. Tsavo where a sudden drought may kill off large numbers of recently born animals (Mr. S. Trevor 1972, pers. comm.).

A third error would be caused by fluctuations in the conception rate and hence birth rate from year to year. This has been demonstrated by Laws (1969a) in large samples collected in widely separated study areas. By examining pregnant cows, and ageing the embryos he showed that conception rates varied greatly from year to year. These fluctuations like the early mortality are short term.

For the above reasons, the birth rate estimated for one year by using the percentage of first years in the population is not a good measure of the steady recruitment of a population.

A much better measurement of fertility can be obtained by recording the actual numbers of calves born to a number of known females over several years. While this is impossible in short-term cross-sectional studies, at Manyara such registration was possible and was employed for four years. Observations were drawn from *25* family units, and every mature female of these families was known and registered by mid-1966. Those that survived the full four year seen numbered 98 in all. In estimating the birth rate by a proportional calculation all those which reached maturity or which died during the study period and otherwise might have produced a calf, have been excluded. On this basis the births were recorded for each year and appear below:

1966–1967	1967–1968	1968–1969	1969–1970
8 (poss. 11)	34 (poss. 35)	22	21

The figures in brackets include calves believed to have been born and to have died before registration.

The minimum number of calves born to these 98 females was *83*, which gives a maximum mean calving interval of 4.6 years, which is equivalent to 21.7 per cent of the mature cows giving birth annually. In fact the calving interval may be shorter for particular individuals. Calving intervals of 3 years, 4 years, 3 years 11 months, 3 years 10 months, 3 years 6 months and 3 years 8 months were also recorded. Although this estimate averages four years of births, the differences in birth rate from one year to the next emphasize the dangers of extrapolating from one or two years of data. If the low birth rate of 1966-1967 had been considered as representative, then the calculated mean calving interval would have been 12 years, whereas the 1967-1968 birth rate gave a mean calving interval of 2.9 years.

Nevertheless, the only data available for comparison comes from cross-sectional studies in which the birth rates and mean calving intervals have been calculated from the proportion of pregnant females in a sample collected in the space of a few months. The Pregnancies in these studies were detected by autopsy (Perry, 1953; Buss & Smith, 1966; Laws, 1966; Hanks, 1972). Since gestation lasts for 22 months (Perry, 1953) the pregnancy ratio embodies two years of conceptions, thus smoothing annual fluctuations to some extent. To obtain results that were strictly comparable with these studies the Manyara data was used in the some way. The breasts of pregnant female's swell up, but pregnancy cannot be detected infallibly this way, instead the number of females pregnant at the mid-point of each year was calculated by counting the number of calves born within 22 months of that point in time. Following previous workers, the proportion of pregnant females was calculated from a total which this time included all females judged to be mature; that is all females estimated to be over eleven years of age (see below). Consequently in this calculation females which died or arrived at maturity during the study period were included in the appropriate years. The results are summarized in the following table:

	Total mature females	**Number pregnant**	**Percent pregnant**
Mid-1966	103	46	45
Mid-1967	105	56	53
Mid-1968	104	46	44
35 year mean	104	48.7	47

To obtain the mean calving interval the proportional formula derived from Perry (1953) is used:

$$\text{Mean Calving Interval} = \frac{\text{Total No. of Females X Gestation}}{\text{No. of pregnant females}}$$

This gives a mean calving interval of:

1966	4.1 years
1967	3.5 years
1968	4.1 years
3 year mean	3.9 years

It will be noted that the mean calving interval obtained by the cross-sectional method is lower than that obtained over the full study period. This is because the pregnancy ratios are calculated from years which had an exceptionally high birth rate.

Nevertheless, the second calculation of mean calving interval is more directly comparable with values obtained for other populations. Out of four populations that Laws (1969a) studied, the Mkomazi population is the most nearly equivalent to Manyara with a calculated mean calving interval of 3.5 years. Laws considers that this may not be representative for the Mkomazi population and that his sampling may have covered a period when there was a temporary surge in conceptions. Using a different method (Laws, 1967), placental scar counts gave an independent check on the mean calving interval suggesting a value of between *4* and 5 years for Mkomazi.

Using these two methods Laws (1969a) tentatively concluded the mean calving intervals as follows:

MK.	4-5years
T.N. P.	6-7years
M.F.P.N.	6-7years
M. F. P.S.	8-9years

This conclusion was later modified (Laws et al. 1970) and will be further discussed. The figure of 3.9 years for the mean calving interval for Manyara obtained from the pregnancy ratio, and the figure of 4.6 years obtained from the actual births per female, put Manyara into line with the Mkomazi peculation. Since Mkomazi was the most fertile population in respect to birth rate yet sampled, Manyara too may be considered to possess a relatively fertile population.

Female age of puberty

Another factor affecting recruitment is the age of attainment of puberty in the female. Laws & Parker (1968) were able to classify females as immature, pubertal, and mature on the basis of macroscopic examination of sliced ovaries, and from this they calculated the mean age at first ovulation for five different populations.

At Manyara estimation of this parameter in a strictly comparable form could not be made in the same way. However, if it were assumed that females became pregnant as soon as they reached the age of puberty then it would be possible to calculate the mean age of puberty by subtracting 22 months from the mean age of first parturition. If this assumption is not true, and there is some delay after the onset of puberty and before conception, then this method will overestimate the age of puberty.

The accuracy of ageing will also greatly affect the estimate. The methods used for age estimations depend on the shoulder height variation with age, and are described in detail in Chapter 3. I have attempted to estimate the mean age at first parturition both in a cross-sectional calculation and by using long term data.

In the first treatment I estimated the ages of all mothers at mid-1970 and lumped them in categories of 5-10, 11-15 and 16 years and over. The table below shows the percentage of all females that had produced at least one calf in their lives.

5-10 years	11-15 years	16 years and over
3%	32%	100%
n = 33	n = 32	n = 92

Since there were no females over 15 years that had not given birth, those results suggest that the mean age of first parturition lies somewhere between 10 and 16 years and it can be concluded that the age of puberty, which must be at least 22 months earlier than first parturition, is less than 14 years.

In the longitudinal method I recorded the age at which young females produced their first calves. All females without any calves at the beginning of the study period, which subsequently had one, were included in this registration, despite the fact that they previously might have had a calf which had died. This source of error would tend once more to increase the estimate of mean age at first parturition. The results appear in the following table:

Table 8.1

Estimated Age of Mother at Birth of First Calf

	8	9	10 ± 1	11 ± 1	12 ± 2	13 ± 2	14 ± 2	15 ± 2	16 ± 2	17 ± 2	18 ± 3 years
No.	1	1	1	5	5	3	3	5	2	1	1

Total = **28**
Median age = 13
Mean age = 13 *(95%* confidence limits ± *.93).*

The mean age at first parturition is 13, which indicates that the mean age of puberty is unlikely to be more than 10-12 years. If however some of the older females were in fact producing their second calves, after the death of their first, then the mean age of puberty is even earlier. Laws (1969b) estimated mean ages of puberty for MK. 11 years, T.N.P. 12.5 years, M.F.P.N. 14 years, M.F.P.S. 18 years, B.C.F.R. 20 years. Once more the Manyara population appears to be very fertile in comparison to other populations. A mean age of puberty of 11 is amongst the lowest recorded, but is near to that of Mkomazi.

It is also interesting to note that the apparent range in age of puberty, from 6 to 16 years, was larger at Manyara than in any of the populations Laws encountered. The explanation for this is almost certainly that the older females in the Manyara sample had previously given birth to calves which had died before registration. Since calf mortality may be as high as 10 per cent in the first year (see later) this is not surprising.

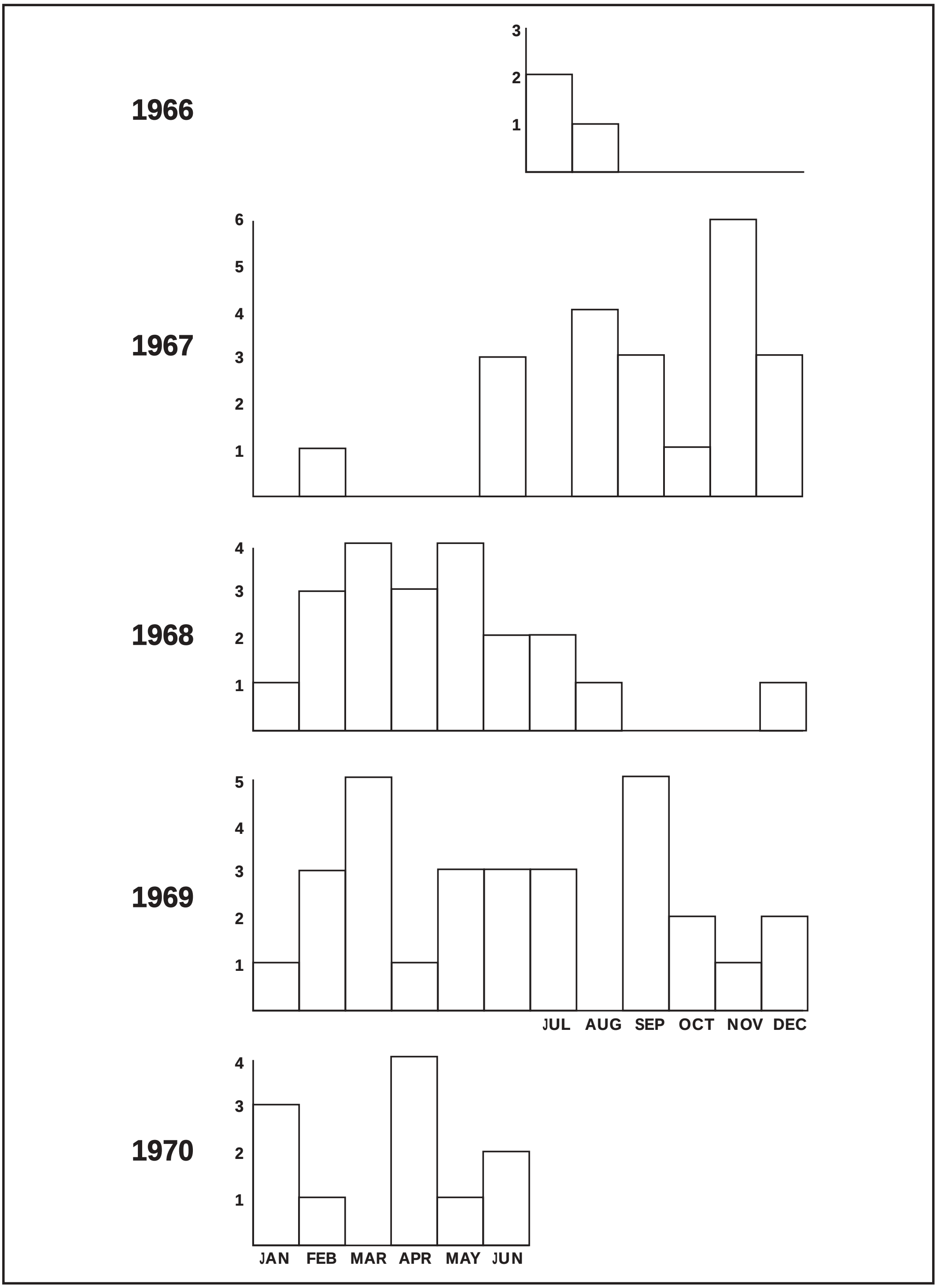
Age of Menopause

Even the largest and presumably oldest females had not stopped breeding. Within *4.5* years each of the seven females of the largest size category, No. *5*, produced a calf, which gave no indication that their fertility was lower than the other females. Nonetheless it has been established in other populations that cow elephants do become reproductively inactive in a manner similar to the human menopause at about the age of 55 (Laws et al. 1970; Laws, in press).

Calving Related to Season

Every time a calf was recorded for the first time, an estimate was made of its approximate date of birth to the nearest month. Since most groups were seen every month the error was small and it was possible to collect 88 birth records which were considered to be accurate to within a month. The results are summarized in Fig. 8.1. Although there appeared to be a

Figure 8.1
Births per month



seasonal difference in some of the years, the combined results of three full years, 1967–1968–1969, showed an apparently random distribution with no evidence of seasonal calving.

The small number of calves in late 1966 and early ‘1967 is probably related to a long-term fluctuation in conception rate rather than to any short term seasonal effect. It is possible that a larger sample would show a significant peak in the rainy season, but it is also possible that in the absence of a large seasonal variation in food and water supply at Manyara, seasonal calving is of no great survival value.

In contrast, other populations studied showed significant calving peaks in the rainy season, which became most pronounced in the areas of most extreme climate, in particular in the Tsavo National Park, Kenya (Laws, 1969a), and in the Luangwa Valley, Zambia (Hanks, 1969).

Conceptions Related to Annual Rainfall

It is possible to relate the large variation in annual birth rate to the rainfall of the year of conception, 22 months previous to the year of birth. Fig. 8.2 shows the rainfall recorded at two stations at either end of the Park from 1961 to 1970. As the conception rates are calculated by counting back 22 months from the birth rate they represent a minimum value, as no allowance is made for abortions, resorption of embryos, or for calves which died before registration. Both the yearly rainfall and the conceptions are calculated from the middle of one year to the middle of the next, thus being separated by the long dry season from June to September in which virtually no rain falls.

It is apparent that the year 1964–1965 had both the lowest rainfall and the lowest number of conceptions, but in the following years the correlation between rainfall and conception is less apparent. This is partly because females following parturition remained in lactational anoestrus for a variable period (Perry, 1953), and so were unavailable for conception. It would be more meaningful to compare the conception rate of available females. A rough estimate of the number of available females in each year can be calculated on the assumption that on average a female undergoes a two year lactational anoestrus following parturition. (This is in accordance with the data on mean calving interval). To obtain the number of available females for the year preceding the study period, it was necessary to assume that the number of mature females remained constant in the years 1962–1964 and that; the conceptions of those years can be calculated from the age structure by allowing for first year mortality at the rate of 10 per cent.

The percentage of available females conceiving appears to be correlated more closely with the rainfall. Table 8.2 below gives the values:

Figure 8.2
Annual rainfall related to conceptions

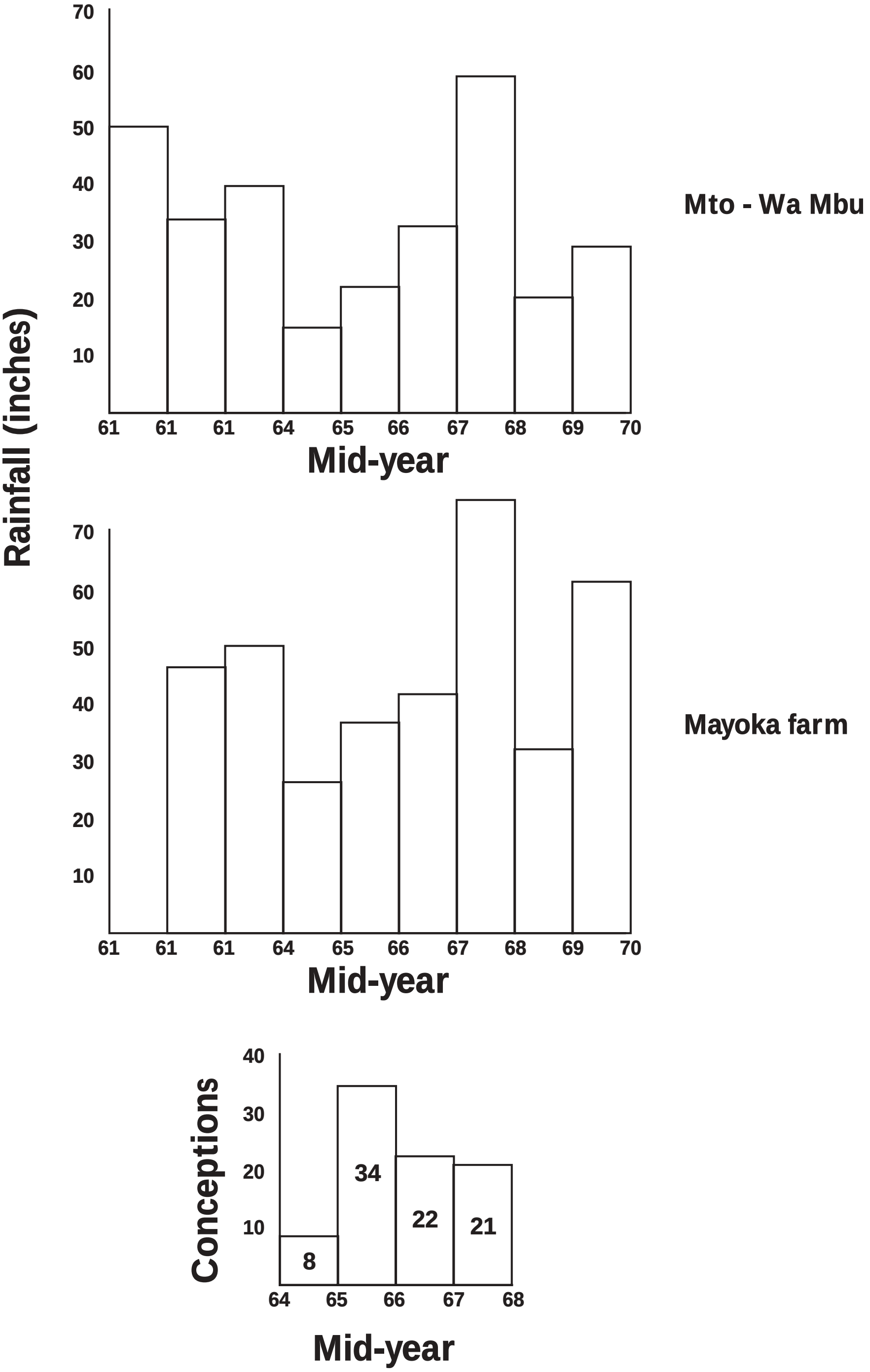


Table 8.2

Conceptions related to rainfall

Year	1964	1965	1966	1967	1968
Conceptions		8	34	22	21
No. available females		70	76	56	42
% Available females conceiving		11	45	39	50
Rainfall inches (Mto-wa-Mbu)		15	22	32	51

The sample size and number of years are too small to allow a statistical treatment, but these figures seem to be in accord with the correlation found by Laws (1969a) between rainfall and conceptions in other populations.

Mortality

Very little is known about the relative importance of different kinds of mortality on elephant populations. Apart from reports of shooting elephants either for sport, ivory, meat, or for crop protection, few quantitative reports exit of the cause of death in the wild. Disease in elephants have been referred to by Laws & Parker (1968) who relate mandibular abscesses to stress and habitat conditions. Arteriosclerosis has been described by McCullagh (1967), and Sikes (1968, 1971) relates it to habit conditions. Anthrax has been reported in African elephants (Savidge, pers. comm.) and the notes on the diseases of Indian elephants (Gilchrist, 1851; Steel, 1885; Evans, 1910), suggest that African elephants like their Asian counterparts are vulnerable to a wide range of disease. A postmortem on one cow, which had been seen dying, discovered a necrotic foetus (Woodley, pers. comm.). Croze (1970) recorded the death of a cow, the cause being B-Haemolytic streptococcus infection of the mucosa. The recent drought in Tsavo (1971-72) suggests that starvation and heat stress may also be important causes of mortality (Trevor, pers. comm.).

Causes

At Manyara only four quantitative records of mortality causes could be made. In the course of patrols, dead elephants were encountered infrequently. At times carcasses were reported by Park rangers or tourist guides, or by the Game Department scouts if Park elephants were shot while raiding crops just outside the boundary. Occasionally a freshly dead elephant could be located by watching the descent of vultures or from the aeroplane.

Altogether fifty-seven carcasses were found within the Park or just outside its boundaries. They were located in varied habitat types and were widely scattered. Apart from the tendency of elephants to run back to the safety of the Park when wounded, there was no indication of any preferred habitat or site as a place to die, contrary to the persistent belief in “elephant cemeteries”.

Some of the corpses had been dead for a long time when found, and were only identifiable by a few pieces of skull - they may have died five years before discovery. Even recently dead elephants were so decomposed when I found them that I could seldom discover the cause of death, and could only recognise four as individuals.

Although the sample size was small, by far the most important cause of death appeared to he human predation. Out of the 42 elephants whose remains were found that died in the study period, 23 (55%) had been killed by man. 13 of these were shot or speared while crop raiding outside the Park, of which 4, when mortally wounded, had managed to regain the Park before dying. 10 were killed within the Park, 9 of these were poached and one was killed by a Ranger in self defence.

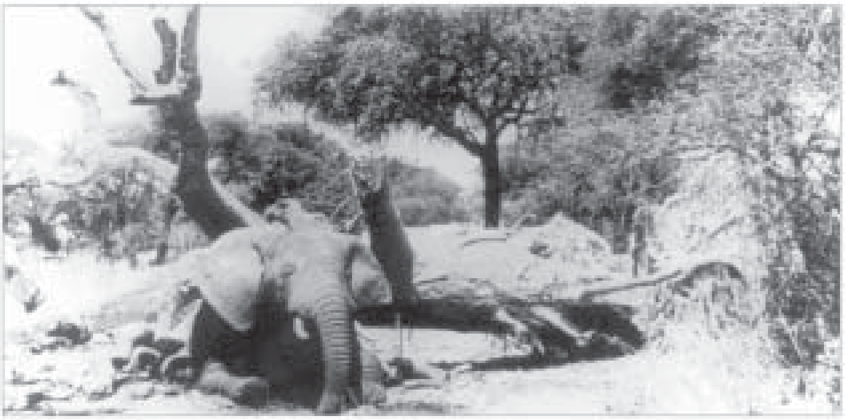
Other than those elephants killed by man, 19 (45%) dead elephants were found. The mortality causes when obvious were as follows. Two calves were killed by lions after being separated from their parents and one calf died of starvation after being orphaned before weaning. One female died of old age when her teeth wore out and another’ cow fell off a cliff and broke her neck. One bull starved to death after becoming stuck in a swamp, and one bull was apparently gored to death by another who pierced his brain with a tusk. The remaining 12 died of causes unknown. Some of ‘them were probably mortally wounded while crop raiding, others had possibly succumbed to disease, but it was not possible to confirm this. In the Tarangire one bull was killed by a falling baobab, which it had been eating (Fig. 8.3).

The Manyara population seemed remarkably healthy. Few elephants seemed out of condition or suffering from disease. A few had growths or abscesses on their heads or trunks but these often sloughed off after a few months. One female was covered with wart-like growths on her trunk, but this was a very rare condition. Typically the thighs, back, shoulder, forelimbs of almost every elephant appeared to be well padded with flesh, in contrast to elephants in poor condition such as those encountered in Tsavo during the 1971 drought, Fig. 8.4 (Mr S. Trevor, 1972, pers. comm.). A retrospective survey of more than 4,000 elephant photographs taken during the study period, showed that almost without exception the Manyara elephants in both wet and dry seasons were in ‘good’ condition, according to Albl’s (1971) criteria.

In the years previous to this study, many elephants were shot around the Park. The first Warden killed any that entered the village of Mto-wa-Mbu or any that attempted to pass North to the forest and

Figure 8.3
Mortality

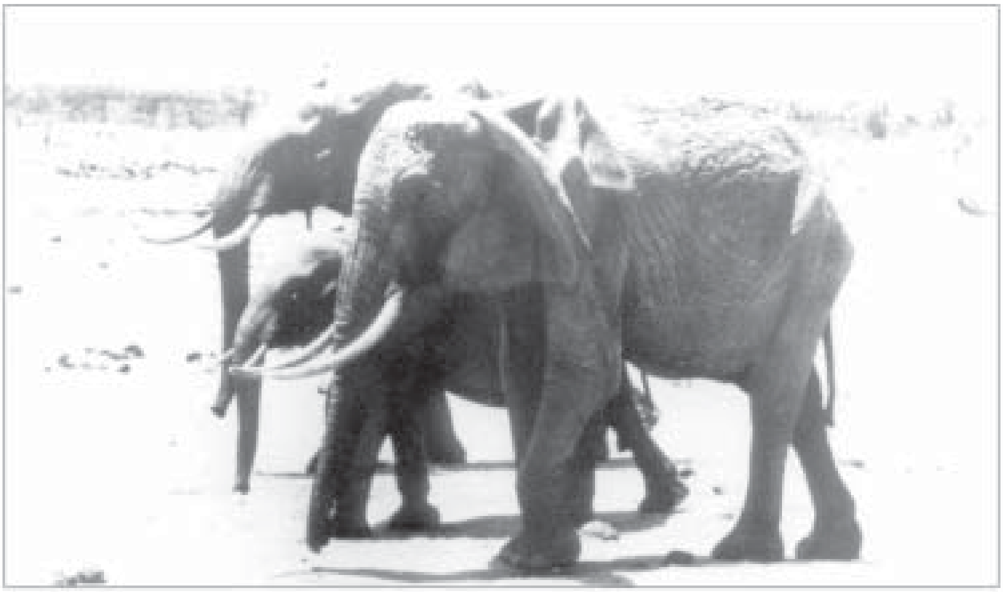
A. **A young bull speared while crop raiding above the Manyara Park, 1970.**



B. **A bull crushed by a Baobab which had been weakened by elephant tusk gouging (Tarangire 1970).** *(Photograph by P. Fera)*

C. **A cow which fell down the Endabash escarpment (Manyara 1970).**

Figure 8.4
Condition of elephants



A. An emaciated cow during the 1971–1972 drought in Tsavo. *(Photograph by courtesy of Simon Trevor)*

B. Manyara elephants in typically "good" condition, 1970.

swamp of Kitete Chini. Exact figures were not kept but it amounted to 5 to 10 per year. This mortality must have represented a large proportion of the annual offtake for the forest groups, which only numbered approximately 50 animals.

In the South even larger numbers were eradicated. Out of an estimated population of 500 in the Magara farms area, an area of about 80 square kilometres immediately to the south of the Park, about 300 were shot in the years between 1955 and 1966 (Mr. C. Thom, pers. comm.). In 1966 alone 60 elephants were wounded or shot on the farm nearest the Southern Park boundaries. The survivors left the area altogether and moved either up to the Marang Forest, or into the Park, possibly doubling the resident population. Now elephants still return there at night from the Park, and about 15 are shot every year. In 1970 seven elephants representing a complete family unit were shot by a heavy calibre sporting rifle 200 yards inside the Southern boundary. Human predation is certainly heavier in the South and exerts a heavier toll on the Southern clan than that suffered by the Central or Forest elephants.

Despite the fact that shot elephants were the easiest to locate and this factor must have increased their proportion in the sample, I consider that shooting is still the major cause of death in this population.

In terms of importance, the mortality causes probably followed the order of human predation > accidents > disease > animal predation and other causes.

Rates

Mortality rates in most animals vary with age (Odum, 1959). Laws (1966, 1969b, in press) has shown that the mortality of most elephant populations can be divided into three phases, early calf mortality, constant adult mortality, and old age mortality, and that in areas of heavy hunting pressure the males with their heavier ivory decline more rapidly.

At Manyara it was impossible to collect enough lower jaws, from which the age could be estimated, to make a meaningful sample. Fortunately, this was unnecessary as mortality rates within the family of units could be measured once more by the method of registration.

The same sample of 25 family units which were observed for natality were also observed for mortality. Mid-1967 was taken as the starting point, by which time all the members had been entered in the filing system numbering exactly 261 animals. Thereafter, until mid-1970, every permanent disappearance of an animal from its unit was registered as a death, unless another explanation could be found. This assumption is justified by the remarkable stability of the family units. Apart from young males at the onset of puberty, no cow or calf, except for one possible exception, was ever seen to leave its unit permanently and join another or wander alone.

In the one example when an animal did leave its unit and apparently join with another in a different area, even then it

Table 8.3
Mortality and survivorship

	0 - 1 yr		1 - 2 yrs		2 - 3 yrs		3 - 4 yrs		4 - 5 yrs		5 - 10 yrs		Over 10 yrs	Total deaths
Mid 1967	10		16		13		23		10		62		130	
		-2		-1							-2	+13	-5	10
Mid 1968	34		8		15		13		23		57		138	
		-2						-1		-1		+11	-6	10
Mid 1969	24		32		8		15		12		68		143	
		-3						-1			-3	+12	-1	8
Mid 1970	23		21		32		8		14		65		154	
Total at beginning of first three years	68		56		36		51		45		187		411	
Total deaths	7		1		0		2		1		5		12	
Combined % yearly mortality	10.3		1.8		0		3.9		2.2		2.7		2.9	

Adult mortality 2.7 %

was seen again near the end of the study. I believe that such behaviour was sufficiently rare to justify the assumption of death in every other example of disappearance, apart from the departure of young pubertal males. Although some units split, the fragments formed new stable groups which themselves could be checked regularly for births and deaths, just as before.

With young males on the verge of puberty, however, there was an element of uncertainty. Their departures could not be regarded as deaths as they normally would leave the group anyway at this age. Out of 15 young males who left their families, 5 were known to survive up to the end of the study period. For the remaining 10 there were no records of sightings which suggests that they either died or changed their range (or may have been overlooked). This uncertainty imposed an upper and lower limit to the calculations of mortality.

The results of registration are summarized in Table 8.3. The annual mortality has been calculated for 7 different age groups. The figures in the body of the table represent the number of animals that were estimated to be in a particular age group at the middle of a particular year. In the 0 - 1 class it has been assumed that three females that were long overdue for calves had in fact given birth but that the calves had died before they had been registered. If this assumption is valid the first year mortality is 10 per cent. Without this assumption first year mortality is 6 per cent. The fluctuations in mortality seen in the higher age classes are probably caused by the small sample size. By pooling 3 years' data for all the non-infants, 786 individual survival records were obtained, which gave an average annual mortality of 2.7%. If the 10 pubertal males that disappeared all died, which is unlikely, the annual mortality of the 781 animals would be raised to 3.9 per cent. As some young bulls may have been overlooked or may have changed their ranges it is reasonable to conclude that the age-specific adult mortality within cow/calf units lay between 3 per cent and 4 per cent per annum. The mortality of independent bulls is unknown but is likely to be higher than that of the cows and calves. Bulls wander farther and are more likely to come into conflict with human interests or to be hunted.

In other areas elephant mortality has been calculated from life tables, the raw data being the age at death of found remains., or from the age structures of living populations or collected samples. Adult constant span mortality of 5.1–6.6 per cent has been suggested for the populations in M. F. P. N., M. F. P. S., B. C. F. R., T. N. P., Q. E. P., Laws (1969b, in press), which is higher than earlier estimates of 4 per cent for Q.E.P. (Laws, 1966), 4 - 5 per cent for M.F.P.N., M. F. P. S., Q. E. P. and T. N. P. (Laws & Parker, 1968), and about three per cent for MK (Laws, 1969b).

Although these rates were calculated by a different method, which in effect covered a longer time span, the Manyara population over a 4–year span had a mortality which was relatively low, and comparable to Mkomazi.

Age Structure

Methods and accuracy of age estimation are described in Chapter 3, and the age structure of 28 family units is summarized in Appendix 4.

The age frequency distribution in June 1970 of both sexes up to the age of 15 is represented in Fig. 8.5. The irregular variations in frequency from one year class to the next shows that the parameters of birth rate and/or early death rate did not remain constant from year to year and may even vary for different age groups. It has already been demonstrated that fluctuations in numbers of calves in the first 4 year classes were caused by variations in the birth rate between 1966 and 1970, possibly connected with rainfall in the year of conception. It is likely that, at Manyara, it is the annual conception rate, which is primarily responsible for the peaks and troughs of the age distribution, rather than mortality. For example, only 8 calves were born from mid 1966-68, compared to 34 calves from mid 1967-68 (cf. Fig. 8. 2). Fluctuations in estimated age frequency distribution have also been a feature of other populations. The Manyara evidence suggests that the modal frequencies in M.F.P.N.., M. F. P. S and T. N. P. are more likely to be caused by cycles in recruitment as suggested by Laws (1969b), rather than mortality, or by inaccuracies in the ageing system (Hanks, 1972).

The age structure re-emphasizes the dangers of drawing any conclusions about fertility from the ratio of first years to adults from one year's data.

The overall age structure of Manyara can be compared with other populations by lumping age groups into five year categories, of 0-5, 6-1O, 11-15, over 15. Fig. 8.6 shows age frequency histograms in which the Manyara population is compared with those of MK., T.N.P., (Voi, Koito, Mackinnon Road), M.F.P.S. M. F. P. N., B.C.F.R. (after Laws, 1969b). It is evident that Manyara with 99 per cent of the individuals within family units under the age of fifteen, once again is closest to Mkomazi. It may be concluded that Manyara has a young and healthy population relative to others.

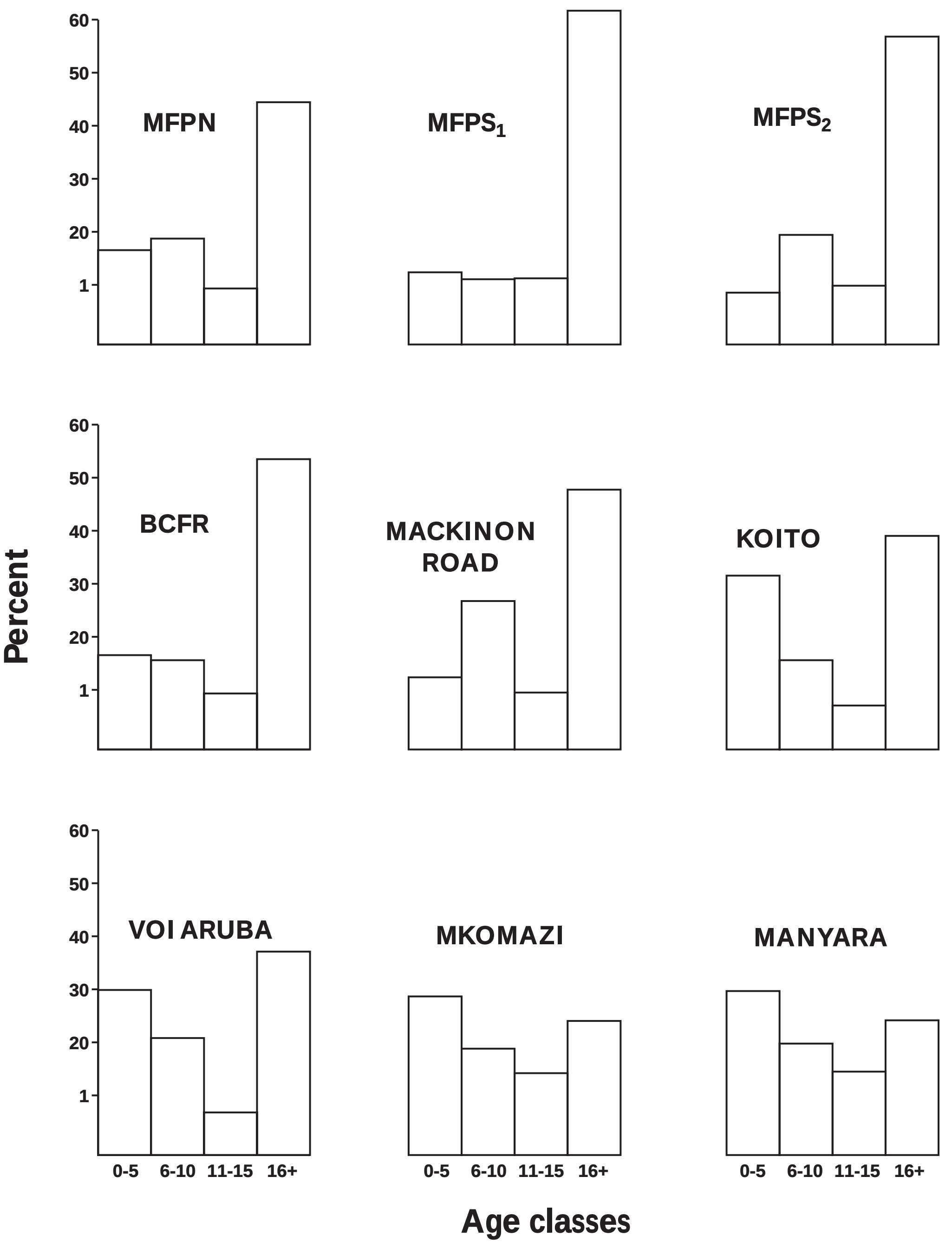
Observed population Growth

As the bulls were independent, population growth could only be calculated for the family unit sample. Appendix 5 summarizes the changes within each family unit and their sizes over four years from mid-l967 to mid-1970. It will be noted that there were 25 family units in the sample at the beginning but three of these split so that there were 28 family units at the end.

There were 261 animals in mid-1967 which after subtracting deaths of members and departures of young males, had increased to 302 animals by mid-1970. Thus the sample population expanded at a mean annual rate of 5.0 per cent over 3 years. However, it has already been suggested that these 3 years were years of relatively high birth rate. The births for 1966-1967 only amounted to 8 calves compared to 34, 24 and 23 in the

Figure 8.5
Age frequency distribution of both sexes (June 1970) up to the age of 15

Figure 8.6
Age classes



subsequent years. If the mean growth rate could have been calculated to include the year of low birth rate the value would be lower. Although the absolute number of this cow/calf sample was not known at mid-1966, it can be extrapolated by applying the known birth rate for 1966-1967, and assuming the calculated adult annual mortality of 3.5 per cent applicable to later years. This calculation suggests that the sample population showed zero growth between mid-1966 and mid-1967 remaining at the level of 261 animals. Consequently the mean annual increase of the ca-vole population over the 4 year span from mid-1966 to mid-l970 is reduced to 3.7 per cent rather than the 5. 0 per cent in the three year span.

Since the sample formed more than 60 per cent of the total population it was probably representative of all cow/calf groups. However, the bulls could not be included in this calculation. Since their mortality was probably higher than the cows and calves It is likely that their numbers increased at a slower rate. Therefore I conclude that the annual growth of the total population was probably between 3 and 4 per cent. This corresponds to an approximately 3.5 per cent increase in the mean corrected registration estimates of population size (Chapter 4, p.52)

This increase in an environment which already appears to be overcrowded makes the possibility of further increase through recruitment a matter of concern. Annual variations in the vital parameters show that any predictions of future population levels based even on four years of observation would only be tentative. However, projections can be useful for other reasons. A stable relative age/frequency distribution can be obtained for the observed parameters, and can be compared with the observed age frequency distribution of the study period. If there is a difference then the parameters in previous years must also have been different from those observed in the study period.

It is also possible to simulate the effect on the population growth of varying one or more of the parameters. By empirical manipulation it is possible to discover the extent by which the observed parameters need be altered to give a stable or declining population. These differences can then be compared with natural variation.

With these limited objectives, I constructed a simple mathematical model which simulated the effect of the existing Manyara parameters of fertility and mortality on the female population size.

Simulated Population Growth

In this model it is assumed that the following parameters apply to all females:

Calving interval	**4.6 years**
Age of female puberty	11 years
Age of menopause	55 years
Early calf annual mortality	10% 0 – 1 year
Adult annual mortality	3.5% 2 – 48 years
Old age annual mortality	20% 48+ years

The birth rate, age at female puberty, early calf mortality and middle age mortality are all mean values which were obtained from the Manyara population by registration. The age of menopause, the year at which old age mortality begins and the rate at which it proceeds, are values calculated by Laws (1969a,b), whose comparative studies showed little variation in these parameters from one population to another. Slight approximations in these last parameters will not affect the projections to a significant degree.

The female age distribution of June 1970 was taken as the population structure for the base year. To obtain values for the number of females in the younger age groups of 1-5 years, where the sexes were not known, half of each age class was assumed to be female.

Females above the age of 15, which had previously been classified into 5 size categories were assigned age classes on the following basis:

Female Size Class	Age Class	Number
1	16 – 20	15
2	21 – 30	24
3	31 – 40	25
4	41 – 50	20
5	51 – 60	8

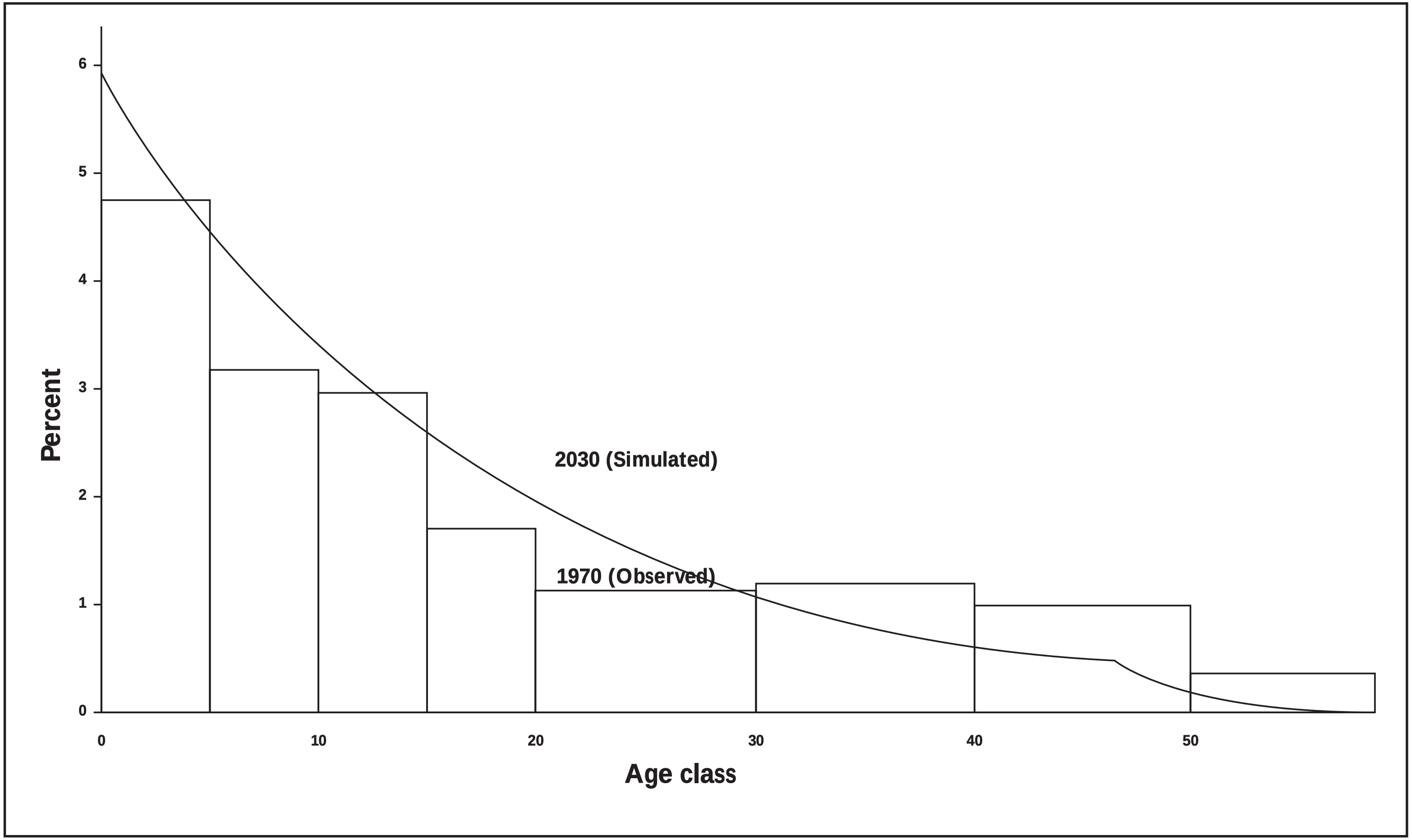
Although this system of ageing is arbitrary above 30 years, once again moderate approximations will not greatly affect the projection, as all females between 11 and 55 are assumed to be fertile producing calves at the average rate, and all females between the age of 2 and 48 are assumed to suffer the same mortality. Therefore if I have incorrectly aged a few animals above the age of 48 it will make little difference to the gross product of calves born each year or to the population total, since their proportion of the total is less than 5 per cent in the base year 1970.

In order to calculate the age structure from one year to the next, the number of survivors from each age class into the next age class was calculated by deducting the appropriate age specific mortality. The gap left by the 0 - 1 years, which had all moved up into the 1 - 2 year class, was filled by the female calves born during the year. The total number of calves born was calculated from the number of breeding females in the first year and the birth rate, and half of them were assumed to be females. From the Manyara age structure of 1970 the programme was set to run for a simulated sixty years (i.e. one potential life span of an elephant).

The female numbers in’ this projection increased from 203 in 1970 to 648 in 2030. The annual increase ratio was 1.8 per cent in 1970/71 and was stable at 2.1 per cent in 2030,

Figure 8.7 shows the proportional change in age structure. The 60 year interval was found to be enough for the population to achieve virtual stability in its relative age frequency distribution. The tendency of a population to achieve a stable relative age structure for a given set of parameters would be expected, according to population theory (Lotka, 1925). It will be noted that the 2030 age distribution included a higher proportion of young age classes than the age structure estimated for

Figure 8.7
Percentage female age distribution



1970. Since some of the females' ages may have been over-estimated in the Manyara sample, it is only worth comparing the proportion of animals from 0 to 15 years, whose ages are known with greater certainty. There remains a difference between the two age structures with 54.7 per cent of the female population under the age of 15 in 1970 compared to 60.3 per cent in the projected population of 2030. This difference suggests that the observed age structure was shaped by less favourable parameters, i.e. higher mortality or lower birth rate, or a combination of the two, in the past, but the 1970 sample size is too small for statistical tests to show significance. It is probable that the rate of increase was lower during the years of lower rainfall preceding the study period, and should conditions become less favourable in the future the population may well stabilize or decline.

The computer simulation also allows empirical manipulation of variables to see what effect the variation of a single parameter, or a combination, would have on population growth. By experimenting, I was able to produce a set of parameters, not far removed from the observed ones, which produced a virtually stable population. The empirically determined parameters were as follows:

Calving interval	**4.6 years**
Age of female puberty	14
Age of menopause	55
Early calf annual mortality	7% 0 – 3 years
Adult annual mortality	4.5% 4 – 48 years
Old age annual mortality	20% 48+ years

When applied to the 1970 age distribution they caused the numbers to drop and then slowly to rise:

Year	Total Females
1970	203
1980	192
1990	188
2000	190
2010	193
2020	193
2030	194
2040	195

This effect was achieved by altering three parameters. The mean age of puberty was delayed by three years, the cumulative early calf mortality was increased from 10 per cent to 21 per cent, and middle mortality was increased from 3.5 per cent to 4.5 per cent. These are relatively small changes which are well within the observed variation within the Manyara population, and it may be concluded that the vital parameters need change only slightly from the values that were observed during the study period to produce a steady or declining population.

Discussion

From the data presented it is evident that Manyara possesses a young elephant population. Despite the relatively high elephant density, the technique of registration revealed a population that appeared to be increasing annually by 3-4%.

There are, however, serious grounds for concern. The environment is steadily being altered in a way that is unlikely to be favourable either to the elephants or to other species. If the present increase continues through immigration or recruitment the woodland destruction can only accelerate. Simulation studies have shown, however, that slight changes in parameters of fertility and mortality could produce stability or decline. The birth fluctuations observed at Manyara show that the parameter of natality is highly variable and there is the suggestion that conception may be inhibited in dry years. Mortality can also be variable as exemplified by the sudden drop in elephant numbers during the recent drought in Tsavo when about one-third of the population in one sector of the Park died within the space of a year (Sheldrick, 1972). The age structure of the Manyara population suggests that these two parameters have indeed moulded the population in an uneven manner in previous years. The favourable years of the study period cannot be considered to be indicative of long-term natality or mortality.

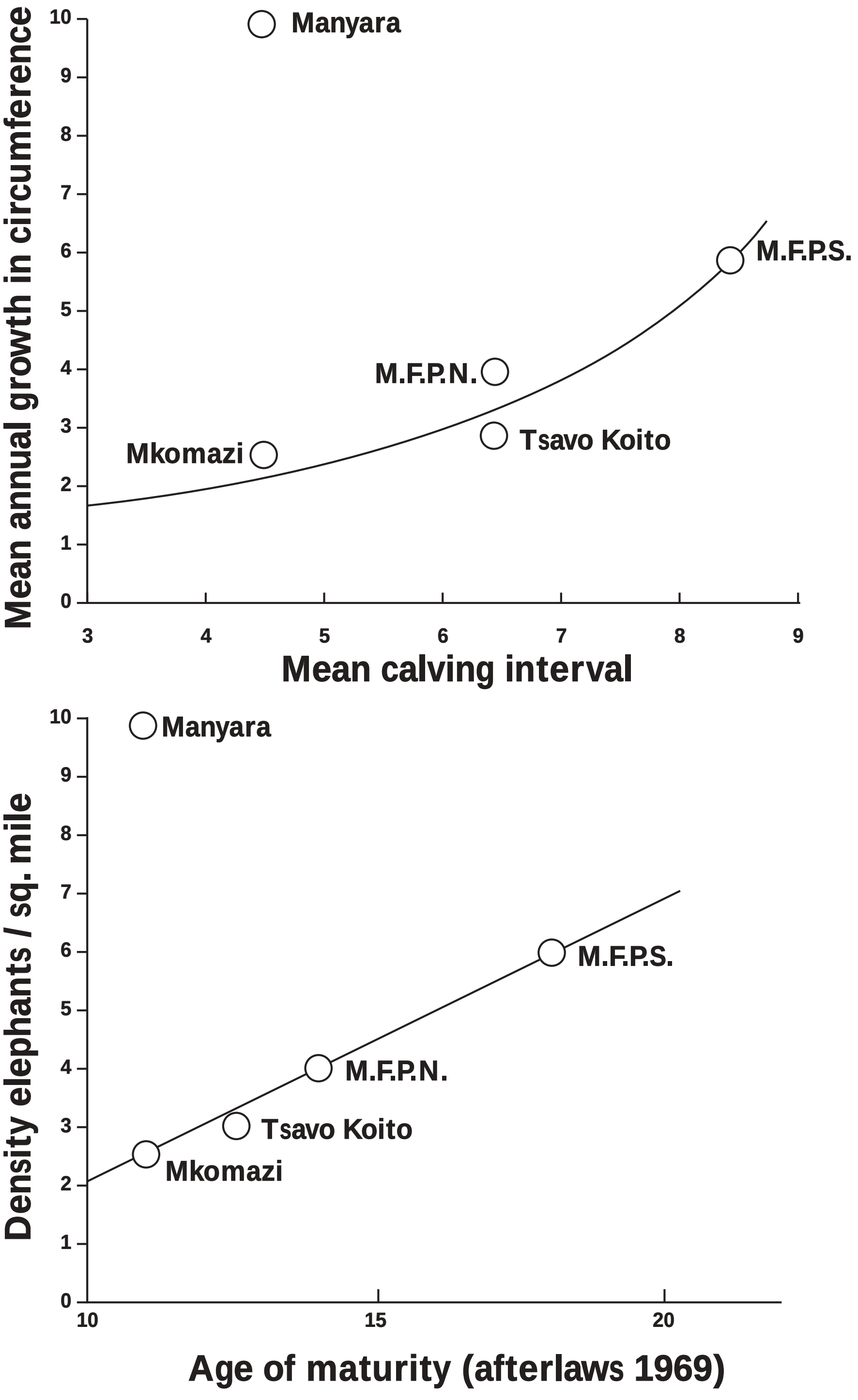
There are few, if any, elephant populations which have not experienced a decrease in range in recent years. No information exists on whether elephants have ever been in balance with their environment, and it is only possible to speculate on the manner in which their populations were naturally regulated before the import of modern firearms and an expanding human population.

From studies in other areas, evidence was collected which suggested that the mean calving interval and mean age of female puberty were directly density dependent (Laws, 1969a, 1970a). In contrast, adult mortality as calculated from survival curves was relatively constant from one area to another (Laws, 1969b, in press).

It was suggested that proximate factors affecting fertility were nutritional deficiencies and heat stress (Laws & Parker, 1968; Laws, 1970a). Both nutritional demands in relation to browse, and shade requirements in relation to canopy cover might be density dependent, as the amount of woodland available would ultimately depend on the density of elephants. However, the data seemed to indicate an even closer fit between fertility and density, which, in view of local differences in carrying capacity, would be difficult to explain in terms of nutrition or shade alone. It was also suggested that social factors might play a part in depressing fertility (Laws & Parker, 1968; Laws, 1969a; 1970b). However at Manyara there was no evidence of social stress despite a high density. Nonetheless under extremes of hardship, it is possible that social stress may truly be encountered in the form of competition for scarce resources. In this case it would be the result of habitat conditions rather than the direct consequence of density.

Fig. 8.8 (after Laws, 1969a) illustrates what he considered to be the probable relationships of mean calving interval and female age of puberty to density. He suggested that in these study areas, there was such a close dependence of fertility on density that “regulatory processes begin to operate at densities above about

Figure 8.8


Mean annual growth in circumference
10
9
8
7
6
5
4
3
2
1
0
Manyara
M.F.P.S.
M.F.P.N.
Tsavo Koito
Mkomazi
3
4
5
6
7
8
9
Mean calving interval
Density elephants / sq. mile
10
9
8
7
6
5
4
3
2
1
0
Manyara
M.F.P.S.
M.F.P.N.
Tsavo Koito
Mkomazi
10
15
20
Age of maturity (afterlaws 1969)

two elephants per square mile”. However the Manyara fertility values, which have been inserted into these diagrams at the appropriate density, do not conform to this model, nor do later estimates in the same study areas made from larger samples (Laws et al. 1970).

The practical implication which follows is that there is no generally applicable density, which can be used as a constant throughout Africa at which elephants are stable and in balance with their environment. In other words an ecosystem with a high primary productivity may be able to support many more elephants, before woodland destruction begins, than one with a low primary productivity. This may seem obvious, but in practical discussions of National Parks policy the figure of 1 elephant per square mile (.4/km^2) is often quoted as a ‘safe’ elephant density. This figure was originally suggested by Darling (1960).

In addition to the effects of habitat on fertility the effect of forms of mortality on the population should be considered. Disease is a possibility in any crowded animal population, and might act in a density dependent manner, although it is likely that sudden but rare epidemics, while reducing numbers sharply (as happened to the buffalo throughout Africa during the great rinderpest epidemic), would only cause excessive “crashes” at long intervals and such oscillations would be less “damped” than those due to other factors.

Another form of mortality which has had great historical consequences for elephant populations, is human predation. It can be argued that formerly human predation was the most important single factor in limiting or exterminating elephant populations. Two types of human predation should be distinguished, the hunting of elephants for meat by primitive methods and the hunting of elephants for ivory using firearms. With the advent of firearms in Africa, shooting by ivory hunters, before the introduction of Game Laws, may have limited elephants below their potential density in areas where they were not actually eradicated. It is difficult to envisage how this shooting might have operated in a density dependent manner as uncontrolled hunting of elephants has usually led to their extinction and not to population balance (Simon, 1962). Primitive hunting on the other hand has existed for thousands of years. Elephant defensive behaviour may even have been evolved largely to counter such predation (see Chapter 5) and in preventing it, the National Parks may have eliminated a most important mortality factor. However, although it is conceivable that this form of hunting might exert a density dependent effect and might have controlled some populations of elephants for periods of time in the past, it seems improbable in view of the range of elephants and the fact that relatively few tribes were elephant hunters that such control would have applied to more than a few populations.

We are left then with the supposition that in the areas where human predation was irrelevant some other form of control existed. With virtually unlimited space and in the absence of human predation, there are three forms of elephant population balance which suggest themselves. The first is a steady population where births equal deaths, and tree regeneration balances destruction of trees. Such a population might be controlled by slight changes in fertility influenced by food availability. Large climatic variations would throw the population off balance.

The second state is a long-term alternating cycle, where the population of the predator depends on that of the prey. In this case, the prey would be the woodland trees and the elephant would be the predator. As the woodlands declined, so would the elephants' density thus allowing regenerating trees to survive to maturity until the depleted elephant population would once again be able to grow, utilizing the new woodlands.

The third model incorporates a mosaic distribution of elephant populations and woodlands, in which the elephants destroy a patch of woodland and then move on to another, being limited in numbers by the number of available patches of trees.

The first model seems the least likely, because' elephant destruction in recent years has been seen to be so rapid even though this destruction is to a large extent an artefact of their constriction. It is more plausible that a combination of the second and third models might have applied.

We are left with the problem of predicting the future of National Park populations. It has to be faced that in removing human predation a significant and ancient form of mortality no longer plays a role. On the other hand if either the second or third models represent the primitive state in the absence of human predation, we have to consider whether we can tolerate such long-term 'natural" cycles within a National Park involving the destruction of huge portions of the habitat with the risk that the elephants, lacking space to escape, may even become locally extinct. As Laws remarked "there is an inherent danger in oscillations for island populations", and the National Parks are in a sense artificially isolated islands.

The future size of the Manyara elephant population cannot be predicted from their current population dynamics. It will depend on the future state of the habitat. Even with a slowing down of recruitment, the high standing crop of mature animals would remain for many years to come, and continue to exert their effect on the habitat. Preliminary vegetation monitoring has suggested that it will be some years before the elephants suffer from a severe depletion of their food supply.

At Manyara the small size of the Park makes the situation particularly dangerous. Fortunately the habitat damage is at an early stage and the experience of other Parks with elephant problems can be watched as they undergo the consequences of laissez faire policies. However Manyara National Park is an extremely small 'island' and much of its charm and value lies in its compact species and habitat diversity. Possible courses of management which would avoid a depletion of these resources are considered in the final chapter.

CHAPTER 9 — DISCUSSION AND RECOMMENDATIONS

DISCUSSION AND RECOMMENDATIONS

Discussion

In summarizing the findings of a research project and its practical applications there is a problem in objectivity. The scientist studying wildlife in his primary role is a specialist who collects facts, analyses trends, and makes predictions in terms of probability. Should his role go further?

In the African wildlife field the scientist as a man is among the well-informed and has been forced to think hard about the problems of policy if only to define the limits of his brief. In the process he cannot help becoming deeply involved. Can he as a man avoid the responsibility of expressing an opinion on policy? I think not, but in expressing an opinion he must make it clear where scientific fact gives way to scientific speculation, and where speculation gives way to opinion.

At Manyara certain facts were plain. There was strong evidence that elephant numbers had risen following a drastic reduction in their range, and had been concentrated in the present Park area and the Marang Forest. The density in the study period of >5 E/Km^2 was among the highest known in Africa and this remained high all around the year. In consequence the frequency of interindividual and intergroup contacts was also relatively high, yet at no level in their complex social organization did this density appear to cause a correspondingly high level of intraspecific aggression or any other form of behavioural disturbance. The apparent lack of territorial behaviour removed one way in which crowding might have led to 'social stress'. Elephant density did however have important consequences. By their feeding habits elephants were definitely affecting one type of habitat, the Acacia tortilis woodland, and these trees seemed to be headed for extinction. However I found that this habitat, although important, formed only one facet of the ecosystem and tree damage elsewhere was light. During the study the diverse Park habitats offered an almost ideal elephant range type and when the dynamics of the elephant population were measured and analysed they showed a young and reproductively active population with a high survival rate. This implied that density in itself did not directly control recruitment in this population under the prevailing conditions.

Less certain but probably true are the following speculations. Comparative evidence from other populations shows that recruitment may decrease through habitat modification. No evidence yet exists that such adjustments can ultimately control an elephant population, though in the absence of range decrease they might (Laws, 1970b). In the short term, even though the woodland damage is at an early stage, Manyara in its present form is probably unviable. We must consider the particularly vulnerable nature of a very small area such as Manyara with its limited capacity to absorb gross ecological change. If the National Parks were to adopt a completely laissez faire policy, a balance between elephants and habitats might come about after large oscillations at some indefinite time in the future, of the order of 100 years, but in the medium term the Park might pass through a denuded phase with few trees, soil erosion, and an elephant population crash. In this connection the development of elephants and habitats in the Tsavo National Park, a vast area where elephants and trees have been left to find their own levels, is of general interest. If violent oscillations in elephant numbers or woodland areas are to be avoided or dampened, this can probably only be achieved either by extending the range available to the elephants or by culling their numbers.

Little is yet known about the control of elephant populations by factors other than man, and while the granting of 'Lebensraum' for elephants or a single swift reduction cull might redress the present imbalance, it is uncertain, and in my opinion even unlikely, that elephants in the habitats at present available will ever co-exist in near perfect balance. However until much more is known about natural regulation by factors other than man there is no necessity to consider continuous yield cropping.

In this connection I reject the view that a reduction in density would speed up recruitment, thus merely postponing the elephant problem; since, firstly, the ultimate cause of all current elephant problems appears to have been a rapid decrease in range of elephants, not an increase in recruitment; secondly, a high density in itself does not appear to decrease recruitment and a low density should therefore not necessarily increase recruitment; and thirdly, the proximate factor affecting recruitment is the state of the habitat and only indirectly density.

Recommendations

In 1965, as a prerequisite to a management policy in the Lake Manyara National Park, I was asked to examine relevant aspects of behaviour and ecology of the elephants. In 1968 Professor Walter Russell formulated draft proposals for .a general management policy for the Tanzania National Parks~ Most of the following recommendations are based on the guidelines provided by his draft.

One of the primary objects of management stated was, ' to conserve the present variety of the different habitats within the Parks and of the different species of fauna using these habitats". A further qualifying clause "to maintain them as nearly as possible in their present distribution and proportions" was dropped. Professor Russell gave his opinion that there was nothing sacrosanct about the numbers and proportions present at any one time. He further recommended that positive management of the biological environment should be used as sparingly as possible".

A somewhat more active policy has been recommended by Professor A.S.. Leopold (1970) when reviewing research policy in the Tanzania National Parks, who commented, “Where animal populations get out of balance with their habitat and threaten the continued existence of a desired environment, population control becomes essential …specific examples include excess populations of elephants in some African parks”. He recommended that a detailed management plan in writing should be formulated to guide the day-to-day administrative decisions. Even so the management policy can only be quite arbitrarily drafted according to opinions on what environment is “desired”.

I believe that culling the Lake Manyara elephants would be a mistake, even though it might arrest the process of deforestation at an early stage. The removal of complete family units, or worse still selective culling, would disrupt the complex social organization which deserves further long term study. I strongly feel, like Laws (1970b) and Sheldrick (1972), that killing programmes are repugnant and should only be undertaken when clearly and urgently needed, Although these authors reach different conclusions about the necessity for culling elephants in Tsavo, the difference of opinion is not yet relevant to Manyara because an alternative exists.

My recommendations for management are as follows:

Firstly, approximately 80 Km^2 of the Southwest shore of Lake Manyara below the escarpment and adjacent to the Park should be restored to its former condition as a wildlife refuge (Fig. 2.4, p.21; Fig, 2.6, p.24). This area until the mid-1950’s formed part of the elephants’ range. At that time it was decided to grant leases to foreigners who had sufficient capital to put in the irrigation schemes necessary to make farming pay on this rather marginal land and to clear the bush. The main object of the alienation was to achieve complete clearance of the bush in order to provide an anti-tsetse belt for the protection of the agricultural development schemes lying well to the south of Lake Manyara. In fact, none of them have cleared the whole of their farms and large areas of bush remain.

The Park’s current problems probably began from the time when the elephants were shot out of this area, the survivors entering the Park. Although the re-allocation of land to animals, rather than man, may seem reactionary, in fact this area could bring increasing economic benefit to local inhabitants if it were managed as a National Park. Most of the farms are in decline. Economic considerations are beyond the scope of this thesis but the success of the present Park and the dependent hotel, with the cultural and economic value which they offer to the village of Mto-wa-Mbu and the nation, stands as obvious justification for this form of land use. In purely ecological terms the Southward extension of the Lake Manyara National Park would give the following benefits.

Adequate range for the elephants: An increase in the population’ s range would allow dispersal, thus easing the elephant density in the present Park area. Continuous elephant pressure on the northern most farms suggest that elephants would disperse swiftly, and if they do so evenly the density in the Park might halve. A lower density of elephants should reduce the mortality of the Acacia tortilis woodlands within the Park and might permit regeneration to keep pace with destruction. Within the farm area recently abandoned sisal fields are covered in young A. tortilis trees, and elsewhere A. tortilis and A. xanthoploea of all age classes arc found widely distributed in dense stands. The forest is equally healthy with a thick undergrowth of young trees. If these were added to the Park ecosystem they could be regarded as a replacement for the woodlands now being destroyed.

Access to the Marang Forest: The Magara area is adjacent to the intact Marang Forest. The access routes from Magara are far better and more numerous than those of the Park. With the three areas united, a balanced ecosystem should be created where a mosaic of woodlands and forest might well reach a dynamic balance with the elephant population. The continued existence of the Park with its present diversity and abundance of species would be much surer.

Water in Dry Years: In the 1961 drought, over a thousand animals from the Park flooded into the area to drink from the river and to use the grazing. The Magara, Garufa and Yambi rivers are more reliable than any of the Park's rivers in dry years, and would provide reserves of grazing for the buffalo on their banks.

If this course is adopted it needs to be done quickly, before alternative forms of land use become too well established in the former range of the Manyara elephant population. I do not believe that this action is merely postponing the elephant problem against a time when elephants will regain their present densities through recruitment. I propose this action as a counter to the imbalance caused by sudden range decrease. No habitat problems have yet been shown to originate from excessive elephant recruitment, and any such build up in numbers would only occur slowly and could be closely followed by a long term monitoring scheme.

Even if further land cannot be acquired the existing ecosystem should not be further disrupted. Any further reduction of the elephants' range should be resisted. The Marang Forest above the Park is a key area (Fig. 2.6, p. 24). At present the Forestry department is tolerant towards elephants but if the Marang Forest elephants were ever harried in any way and forced into the Park the elephant problem in Manyara could quickly become an acute crisis. Numbers would increase to at least 600 elephants and the Park population might even double. The Marang Forest is also vital both as a catchment area and as a buffer food reserve, particularly in times of drought. During the 1961 drought it was reported that many elephants left the Park and climbed up the escarpment into the reserve (Morgan Davies, 1961). At present the timber production is of no more than local value (Mr. W. Carmichael, pers. comm.) and so elephant damage does not conflict with timber production. The forest is maintained primarily as a catchment area. It is important that the National Parks management should closely liase with the Forestry Department in the future management of this area. For instance, experience in the Park suggests that in order to avoid increasing elephant damage within the Marang Forest, the Marang-Eyasi elephant migration route should be kept open (Fig. 2.6, p.24) and villagers cultivating in that area should be encouraged to leave a corridor for the elephants.

Should the Park fail to be extended and should the destruction of trees be judged intolerable, then culling of elephants cannot be ruled out as a possible course of management. If this is decided upon at Manyara, then it should be done by the method of Laws & Parker (1968) which causes relatively little disturbance to the population, since family units are eliminated with no survivors. Selective killing of certain individuals or age classes, e.g. the sick, the weak, the aged, would cause distress and disturbance to the survivors which would far outweigh the uncertain benefits. If the unpleasant decision to cull becomes unavoidable at Manyara, I would recommend that the Central and Northern clans should be left intact to avoid disruption of their social organization as much as possible and the Southern groups, most of which are probably recent invaders, should be reduced.

The question that immediately arises is would the removal of elephants from one portion result in the even dispersion of elephants at a lower density throughout the Park? I believe it would, since elephants are opportunistic feeders and constantly move to find their food. If quantities of regenerating browse became available in the South, where elephant pressure has been reduced by culling, the Central elephants, which anyway use the South as part of their range, would spend more time there consuming the palatable new growth. The exact size of the cull should be determined by the current rates of damage to the woodlands, and could only be approximate calculations. It would be better to over-cull rather than under-cull, so that the process need not be repeated, thereby setting up demands for elephant products and pressure for continuous yield cropping. As stressed before a cull should be regarded as an emergency measure to reduce the excessive density caused by decreased range. At the present state of knowledge there would be no justification for continuous yield cropping, which would be incompatible with the National Parks objectives discussed by Russell (1968).

In order that the Park authorities should be informed about precise rates of habitat change, research should be continued as an essential, monitoring service. I would list future research priorities in the following order:

Firstly woodland and forest dynamics should be enumerated periodically. Regular semi-randomized P. C.Q. transects, repeated at two year intervals, could be carried out by junior staff under supervision and could be used to calculate rates of change with known confidence limits starting from the baseline established in this study. This is the most essential research needed and can be performed at virtually no extra cost with the organization of the Scientific Officer Northern region.

Gross changes can also be effectively monitored by repeating the excellent aerial photographic coverage of 1970. This method should also be extended to monitor the serious erosion problems in much of the Western catchment area of the Park.

As a special study the age structure, growth rates, and factors affecting regeneration of the commonest tree species and those which suffer most damage should be investigated in order to ascertain if recruitment is likely to compensate for decline. In view of annual variations the growth studies would need to cover at least five years to obtain meaningful data. In this connection the growths of certain individual Acacia tortilis trees first measured in 1967 should be followed up.

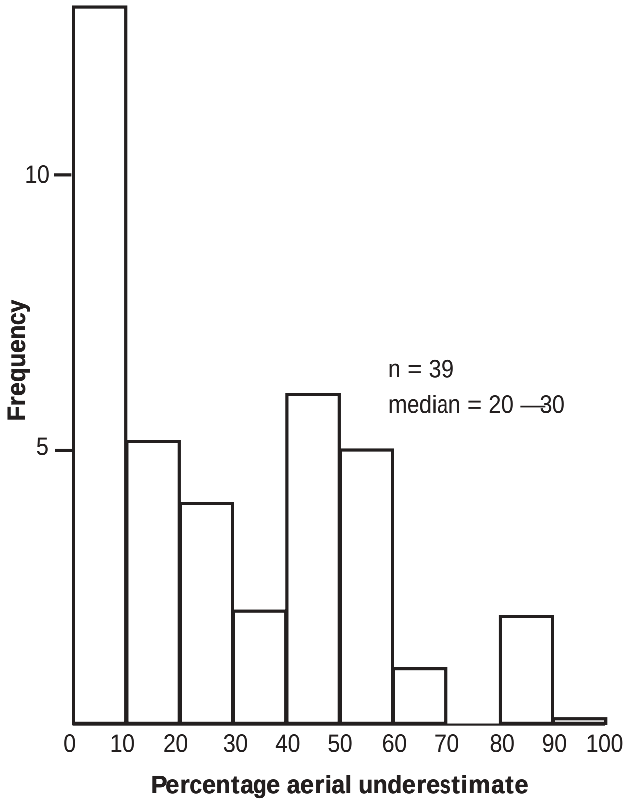
The elephant population dynamics in relation to their food supply is of great general interest in view of possible future adjustments in the reproductive parameters. The same known individuals could be used to monitor trends thus continuing a longitudinal study which began in 1966. Much of this work could also be carried out at low cost by junior staff or a research student once they had learned to use the individual recognition system.

All in all I feel that one of the most valuable results of my admittedly exploratory study is that, together with the work of Lamprey, Laws, Vesey-Fitzgerald, and many others, it has provided a basis of knowledge, and a clearer view of monitoring needs and methods, which could, at relatively low cost, steer future work into effective channels. Much of the funds and effort which have gone into these preliminary studies would be underexploited if the further course of events were not closely scrutinized. I hope that knowledge of the wild African elephant and its ways will increasingly delight and fascinate the people of Tanzania with whom the elephant shares the land. If it continues to live under tolerant but wise protection the elephant will further enrich the culture of its nearest intelligent neighbour, Man.

Appendix 1

Estimates of elephant numbers in small blocks made from air and ground, within less than 30 minutes of each other.

Air	Ground	Air	Ground	Air	Ground	Air	Ground
7	7	10	12	19	31	10	12
17	17	13	13	12	12	8	7
15	17	10	17	14	14	105	106
7	7	8	9	33	41	8	8
40	90	15	17	12	20	13	23
12	12	6	20	21	41	10	19
8	11	10	11	24	41	2	17
3	7	4	20	15	20	12	17
13	13	6	13	45	45		
12	12	5	14	12	19		



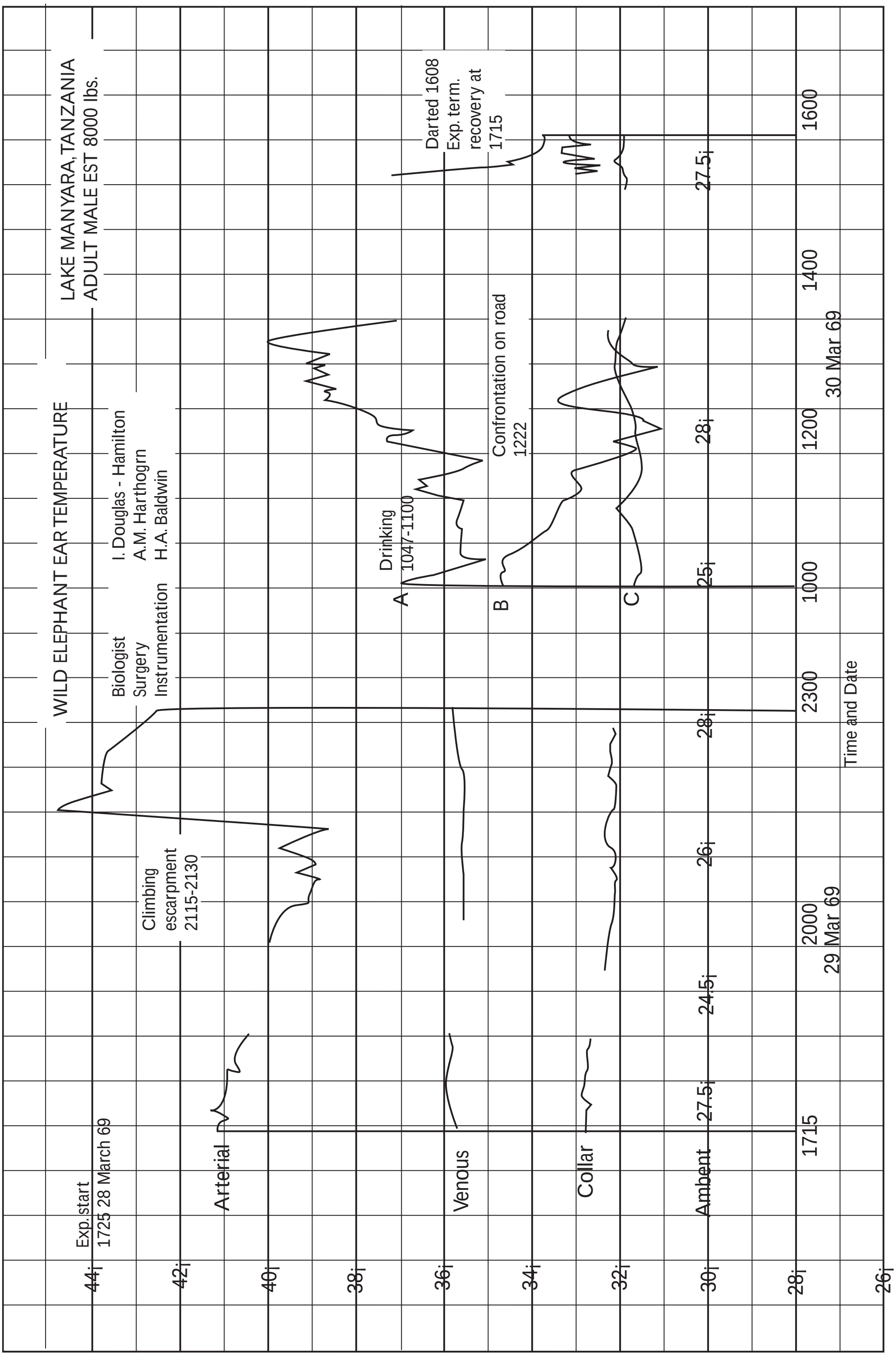
Appendix 2

Temperature of Arterial and Venous Blood in an Elephant's Ear

It has been suggested that diurnal movements of elephants are largely related to the need to regulate their temperatures (Buss, 1961), and that the ears act as cooling surfaces for the blood (Buss & Estes, 1971). Elephants have also been observed regurgitating water, and spraying it over their bodies in circumstances where water was not otherwise available (Gordon-Cumming, 1850; Bell, 1905; S. Trevor, pers. comm.; H. Lamprey, pers. comm.; Sheldrick, 1972), usually when the elephants had been chased or were under some form of heat stress.

At Manyara elephants always moved into the shade in hot weather, as they do in other areas. A telemetry experiment was made jointly with Dr. Howard Baldwin, in order to measure the temperature of arterial and venous blood in the ear. Baldwin (1971) has described the instrumentation, and method of implanting transmitters with thermistor probes suitable for insertion in the lumen of an artery and vein in the ear. The figure rep resents venous and arterial temperature recordings in the ear of a mature bull, made automatically in the field. On the 29th March 1969 after immobilization and implantation of the probes the arterial temperature recordings showed a gradual decrease from 41.2°C., at 17.15 hours when the antidote was administered, to 38.6°C. at 21.15 hours. The venous temperature recordings remained steady between 35.4 and 35.8°C. At 21.15 hours the elephant reached the foot of the escarpment, and began to climb up it, soon vanishing beyond the range of our torches. The arterial temperature readings increased rapidly, presumably as a result of the bull's extra exertion, reaching a maximum of 44.8°C. The difference at this point between venous and arterial temperature recordings was 9.4 °C. On the second day both temperature recordings were lower, possibly due to some clotting and blockage of the blood vessels.

The arterial temperatures seem surprisingly high and since it was not possible to repeat the experiment or switch the probes these results are inconclusive by themselves however the technique has been shown to be practicable and it is hoped to repeat these experiments.


WILD ELEPHANT EAR TEMPERATURE
LAKE MANYARA, TANZANIA
ADULT MALE EST 8000 lbs.
Biologist
Surgery
Instrumentation
I. Douglas - Hamilton
A.M. Harthogrn
H.A. Baldwin
Exp.start
1725 28 March 69
Climbing escarpment 2115-2130
Drinking 1047-1100
Confrontation on road 1222
Darted 1608
Exp. term.
recovery at
1715
A
B
C
Arterial
Venous
Collar
Ambent
44°
42°
40°
38°
36°
34°
32°
30°
28°
26°
27.5°
24.5°
26°
28°
25°
28°
27.5°
1715
2000
29 Mar 69
2300
1000
1200
1400
30 Mar 69
1600
Time and Date

Appendix 3

Appendices 3.1 – 3.8 record the numbers and percentages of times that each individual was observed standing nearest to others, out of the total number of times that each individual was observed. Five separate family units are included, and the results are illustrated in sociograms in Chapter 5.

Appendix 3.1

NEAREST NEIGHBOUR RELATIONSHIPS
(calves excluded)

FAMILY UNIT VICTORIA NO. 31 – 1968

	F1	F2	F3	F4	F5	F6	Total
F1 VICTORIA Is nearest to:		43.90% 18	34.15% 14	9.76% 4	4.88% 2	7.32% 3	41
F2 MARY	50.00% 21		19.05% 8	16.67% 7	14.29% 6	0	42
F3 KALI EARS	52.78% 19	22.22% 8		22.22% 8	2.78% 1	0	36
F4 INNOMINATE	30.00% 9	30.00% 9	13.33% 4		26.67% 8	0	30
F5 GUENEVERE	1.82% 1	3.64% 2	5.45% 3	14.55% 8		74.55% 41	55
F6 SHT. ASSYM.T	1.56 1	0	4.69% 3	8	93.75% 60		64
MKALI	1	1	0	12	0	0	268

Appendix 3.2

NEAREST NEIGHBOUR RELATIONSHIPS **15th August 1970**
(calves excluded) **17th August 1970**

FAMILY UNIT VICTORIA NO. 31 – 1970 **18th August 1970**

	F2	**F3**	**F4**	**F5**	**F6**	**F7**	**Total**
F2 MARY Is nearest to:		53.33% 8	6.67% 1	0	0	40.00% 6	15
F3 KALI EARS	33.33% 6		33.33% 6	0	0	33.33% 6	18
F4 INNOMINATE	5.00% 1	30.00% 6		10.00% 2	0	55.00% 11	20
F5 GUENEVERE	0	40.00% 2	0		60.00% 3	0	5
F6 SHT. ASSYM.T	14.29% 1	14.29% 1	0	42.86% 3		28.57% 2	7
F7 MKALI	23.81% 5	19.05% 4	52.38% 11	0	4.76% 1		21
12” MALE	56.25% 9	25.00% 4	0	0	0	18.75% 3	16
							102

Appendix 3.3

NEAREST NEIGHBOUR RELATIONSHIPS **2nd August 1970**
(calves excluded) **13th August 1970**
FAMILY UNIT LEONORA NO. 31 – 1970 **9th August 1970**

	F1	**F2**	**F3**	**F4**	**Bull**	**Total**
F1 LEONORA Is nearest to:		50.00% 19	26.32% 10	21.05% 8	2.63% 1	38
F2 SLENDER TUSKS	31.15% 19		37.70% 23	29.51% 18	1.64% 1	61
F3 DEEP CUP	16.33% 8	48.98% 24		32.65% 16	2.04% 1	49
F4 V-NICK	23.21% 13	44.64% 25	26.79% 15		5.36% 3	56
						204

Appendix 3.4

NEAREST NEIGHBOUR RELATIONSHIPS
(calves excluded)
FAMILY UNIT RHEA NO. 25 – 1970

	RHEA	**F1**	**F2**	**Total**
RHEA		68.00% 17	32.00% 8	25
F1	73.08% 19		26.92% 7	26
F2	75.00% 15	25.00% 5		20

Appendix 3.5

NEAREST NEIGHBOUR RELATIONSHIPS

(calves excluded) **16th August 1970**
FAMILY UNIT OF OLD NO. 21 **2nd September 1970**

	F1	F2	F3	F4	F5	Total
F1 PROTOTYPE		42.31% 11	0	26.92% 7	30.77% 8	26
F2 BIG	23.33% 7		40.00% 8	33.33% 7	3.33% 6	30
F3 SPLAYED	24.00% 6	40.00% 10		28.00% 7	8.00% 2	25
F4 SMOOTH	25.00% 7	32.14% 9	17.86% 5		25.00% 7	28
F5 NEW	40.00% 10	24.00% 6	4.00% 1	32.00% 8		25
SPLAYED IMMATURE	5.88% 1	29.41% 5	23.53% 4	29.41% 5	11.76% 2	17

Appendix 3.6

NEAREST NEIGHBOUR RELATIONSHIPS **11th August 1970**
(Calves Excluded) **17th August 1970**
FAMILY UNIT FLORENCE NO. 32 **18th August 1970**

	F1	F2	F3	F4	Bull	Leonora's group	Total
F1 FLORENCE		35.71% 15	47.62% 20	16.67% 7	0	0	42
F2 ASYM. TUSKS	38.10% 16		26.19% 11	23.81 10	9.52% 4	2.38% 6	42
F3 ZENOBIA	54.76% 23	19.05% 8		14.29% 6	7.14% 3	4.76% 11	42
F4 CRUMPLED EARS	18.18% 6	45.45% 15	24.24% 8		12.12% 4	0	33
127/11 IMMATURE	29.63% 8	22.22% 6	25.93% 7	18.52% 5	3.70% 1	0	27
C1 ANNA	80.00% 16	15.00% 3	0	5.00% 1	0	0	20
BULL	0	0	0	0		100.00% 2	2

Appendix 3.7

NEAREST NEIGHBOUR RELATIONSHIPS OF CALVES WITH ALL MEMBERS OF THE FAMILY UNIT
FAMILY UNIT LEONORA NO. 9 - 1970 2nd August, 13th August, 9th August

	F1	F2	F3	F4	(A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	Bull	Total
CI LEONORA (B) 5$^{1}/_{2}$ yr.	13.04% 3	4.35% 1	0	0	47.83% 11		4.35% 1	13.04% 3	8.70% 2	0	0	4.35% 1	4.35% 1	23
C'69 LEONORA (C) 6 yr.	40.00% 10	12.00% 3	4.00% 1	0	0	8.00% 2		16.00% 4	4.00% 1	4.00% 1	8.00% 2	4.00% 1	0	25
C2 SLENDER TUSKS (D) 6 yr.	2.63% 1	2.63% 1	15.79% 6	0	2.63% 1	5.26% 2	2.63% 1		26.32% 10	7.89% 3	18.42% 7	10.53% 4	5.26% 2	38
SLENDER TUSKS (E) 2 yr.	0	39.53% 17	9.30% 4	4.65% 2	2.33% 1	6.98% 3	4.65 2	18.60% 8		4.65% 2	6.98% 3	2.33% 1	0	43
CI DEEP CUP (F) 2 yr.	0	4.65% 2	27.91% 12	2.33% 1	2.33% 1	2.33% 1	2.33% 1	13.95% 6	4.65% 2		32.56% 14	4.65% 2	2.33% 1	43
C'69 DEEP CUP (G) 1 yr.	2.38% 1	4.76% 2	47.62% 20	0	2.38% 1	2.38% 1	2.38% 1	4.76% 2	14.29% 6	14.29% 6		4.76% 2	0	42
CI V-NICK (H) 3 yr.	0	3.23% 1	3.23% 1	58.06% 18	3.23% 1	0	3.23% 1	12.90% 4	6.45% 2	3.23% 1	3.23% 1		3.23% 1	31

Appendix 3.8 NEAREST NEIGHBOUR RELATIONSHIPS OF CALVES TO ADULT FEMALES

	LEO	SLT	DEEP CUP	V-NICK	Total
TWO HOLES 11 YEARS	41% 14	18% 6	23% 8	18% 6	34
C1 LEONORA 5 1/2 YEARS	70% 21	3% 1	7% 2	20% 6	30
C'69 LEONORA 1 YEAR	75% 24	19% 6	6% 2	0% 0	36
C2 SLENDER TUSKS 6 YEARS	6% 2	38% 12	50% 16	6% 2	32
C1 SLENDER TUSKS 2 YEARS	0% 0	77% 27	23% 8	0% 0	35
C1 DEEP CUP 2 YEARS	5% 2	29% 12	61% 25	5% 2	41
C'69 DEEP CUP 1 YEAR	3% 1	17% 7	75% 30	5% 2	40
C1 V-NICK 3 YEARS	0	15% 5	12% 4	73% 24	33

Appendix 4

AGE STRUCTURE OF 28 FAMILY UNITS - JUNE 1970

Family Units		AET	HEC	ANI	ATD	APH	ARI	BOA	ISA	JEZ	LEO	CAT	JAG	HEL	HF3	CLY	DEI	JOC	MAR	LED	OLD	OPH	SAR	RHE	POR	ASS	SPH	VIC	FLO	
		01	02	03	04	05	06	07	41	08	09	10	11	12		13	15	18	19	20	21	22	24	25	26	40	27	31	32	Total
sise	5	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	2	0	8
Classes	4	1	1	1	1	1	1	2	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	0	0	1	1	1	20
	3	1	0	2	0	1	1	1	1	2	0	1	0	0	0	1	2	1	1	0	2	1	1	1	1	0	1	1	2	25
	2	1	0	0	2	0	2	2	0	1	1	0	1	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	1	24
	1	2	01	1	1	1	0	0	0	0	1	0	0	0	0	1	1	2	0	0	0	0	0	0	0	1	1	1	1	15
Age	14 - 15	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	4
Classes	13 - 14	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	7
	12 - 13	1	0	0	0	1	1	0	0	0	0	2	0	1	0	1	0	0	1	1	1	1	0	0	1	0	0	0	1	13
	11 - 12	2	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2	0	0	0	1	0	1	1	0	0	1	1	0	11
	10 - 11	0	1	2	0	1	1	2	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	12
	9 - 10	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	9
	8 - 9	2	0	1	0	0	1	0	0	0	0	0	0	0	0	2	2	0	2	0	1	0	0	0	0	0	0	1	0	12
	7 - 8	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	1	10
	6 - 7	1	1	2	0	1	1	2	0	0	2	2	0	0	0	0	0	1	0	0	1	1	0	0	2	1	1	2	1	22
	5 - 6	2	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	1	1	1	12
	4 - 5	0	0	1	0	0	1	0	0	1	0	0	0	0	0	2	0	2	2	1	2	0	0	0	0	0	0	1	0	14
	3 - 4	1	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	8
	2 - 3	0	0	0	2	2	2	2	0	2	2	1	1	1	1	0	2	1	0	0	1	0	1	2	1	1	2	3	2	32
	1 - 2	2	0	3	1	0	4	0	2	1	1	0	0	1	0	1	1	1	0	0	0	1	0	0	2	0	0	0	0	21
	0 - 1	1	1	0	0	1	1	1	0	0	1	1	1	1	0	0	1	2	2	1	3	0	1	0	0	0	2	2	0	23
Total		17	4	14	9	9	21	18	5	12	13	8	6	8	2	11	12	19	9	5	16	9	9	8	9	4	13	20	12	302
Mother/offspring units		6	1	4	4	3	7	6	2	4	4	2	2	3	1	4	4	7	2	1	5	3	4	3	3	1	4	6	5	101

Appendix 5 Change in size of family units - 1967-70

Groups' Names & Code Numbers	Mid '67	Deaths	Births	Departures ♀♀	Mid '68	Deaths	Births	Departures ♀♀	Mid '69	Deaths	Births	Departures ♀♀	Mid '70	3 year totals Deaths	Births	Departures ♀♀
AET (1)	20	3			17		3		20	2	1	2	17	5	4	2
HEC (2)	3				3				3		1		4		1	
ANI (3)	12	1	1		12	1	3		14				14	2	4	
ATD (4)	8	2	2		8		1		9				9	2	3	
APH (5)	8		2		10			1	9	1	1		9	1	3	1
ARI (6)	15		2		17	1	4		20		1		21	1	7	
BOA (7)	22		2	2	22	1	2		23		1	1	18	1	3	3
ISA (41)	–				–				–				5		2	
JEZ (8)	9		2		11		1		12				12		3	
LEO (9)	9		2		11		2		13				13		4	
CAT (10)	7	1	1		7				7		1		8	1	2	
JAG (11)	5		1		6			1	5		1		6		2	1
HEL (12)	7		2		9	1	2		8				8	1	4	
HF3	–				–				2				2			
CLY (13)	10				10		1		11				11		1	
DEI (15)	11		3		14	2	1	2	11		1		12	2	5	2
JOC (18)	15		1		16		1		17		2		19		4	
MAR (19)	7				7				7		2		9		2	
LED (20)	9				9	2		3	4		1		5	2	1	1
OLD (21)	12		1		13				13	1	4		16	1	5	
OPH (22)	8				8		1		9				9		1	
RHE (25)	7		2		9				9	1			8	1	2	
SAR (24)	9		1		10			1	9	1	1		9	1	2	1
POR (26)	11	1	1		7		2		9				9	1	3	
ASS (40)	–		1		5	1			4	1	1		4	2	2	
SPH (27)	10		2		12			1	11		2		13		4	1
VIC (31)	16		3		19				19		2	1	20		5	1
FLO (32)	11		2		13				13	1			12	1	2	
TOTAL	261	8	84	2	285	9	24	9	291	8	23	4	302	25	81	15
MEAN	10.4				11.0				10.8				10.8			
NO. of FUs	25				26				27				28			

Appendix 6.1

Probability of sighting other elephants within 1 Km. Radius of mature bull.

Season	Bulls only	Family unit(s) only	Bulls and family unit(s)	None	Total No.	
Wet	52	11	20	17	613	Frequency %
Dry	50	12	23	21	356	

Appendix 6.2
Frequency of bulls seen per ground encounter.

Time of year	Number of bulls per encounter										
	1	2	3	4	5	6	7	8	9	10	
Wet season	265	98	64	41	21	9	2	6	1	1	Frequency
Dry season	202	92	49	27	17	10	5	1	1	1	

Appendix 6.3
Group size frequency from the air.

Season	Group size classes									
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	>40	
Wet	175	118	56	31	12	17	5	8	6	Frequency
Dry	55	60	27	10	1	7	2	0	2	

Appendix 6.4

Group size frequency in open areas (North and Douth ends of the Park)

Season	Group size classes								
	1-5	6-10	11-15	11-20	21-25	26-30	31-35	36-40	
North end of The Park	135	117	141	26	13	16	6	4	Frequency
South end of The Park	89	64	22	16	2	8	1	4	

Appendix 6.5

Inter-group nearest neighbour distances from the air.

Season	Distance from nearest neighbour, Km.									
	0-0.25	0.26-0.50	0.51-0.75	0.76-1.00	1.01-1.25	1.26-1.50	1.51-1.75	1.76-2.00	>2.00	
Wet	53	97	45	35	19	13	10	10	18	Frequency
Dry	32	88	33	26	20	13	10	9	26	

Appendix 6.6

Frequency of family units seen per ground encounter (within <1 Km.)

Time of year	Number of family units per encounter																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
Feb. - May (wet season)	275	142	85	36	25	16	12	12	7	5	2	1	2	1	0	1	Frequency
June – sept. (dry season)	267	151	60	41	39	23	10	1	5	4	4	2	0	0	0	0	
Oct. – Jan. (wet season)	175	87	52	22	16	8	9	6	6	1	3	2	0	2	2	0	

Appendix 7

Radio–tracking of Elephants

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S. A. CSIR, 1971

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RADIO TRACKING OF ELEPHANTS

by

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Synopsis

As a result of radiotracking it was possible to improve the range maps made from standard ground observations for the three groups at Manyara. The new maps showed that although the elephants kept mainly within the Park they did occasionally venture outside. This data is of great significance to the National Park's management. The maps also showed that even, though they were hemmed in by human settlement on three sides and by a Lake on the fourth side, the elephants did not use all the land that was available to them.

It has been shown that the movements and ranges of elephants vary greatly not only from area to area but also from one individual to another. It seems likely that the factors controlling these differences are related to the nutritional requirements and "wildness" or "tameness" of the individuals concerned.

Radio tracking of elephants

In the absence of hard data, there have been many speculations about the movements of elephants. In some areas, it has been asserted that elephants migrate 480 - 640 km (300 - 400 miles) in their search for suitable food. (See refs. Sikes 1970). The largest movement reported in the literature as definite is over 185 km (115 miles). (Wing & Buss 1970). More recently it has been suggested on the basis of aerial counts that their movements are comparatively small and that no elephants have a range that is more than approximately 48 km (30 miles) across, or of 50-260 Km^2 in area (Laws 1969 & 1970)

Between 1968 and 1970 1. Douglas-Hamilton radiotracked three elephants in the Lake Manyara National Park, one in the Tarangire National Park and one with Dr. Croze in the Serengeti National Park, as part of a five year research programme on the ecology and behaviour of the African elephant.

The objectives were to record movements and ranges in very different habitat types, and also within Manyara to compare differences between individuals of both sexes and varied temperaments. The three animals in Manyara were already well-known and it was hoped to increase the accuracy of the available range maps by following the radiotagged animals into areas of dense bush that normally made observation impossible.

Method

Immobilizations were made with M99 (Reckitt and Colman) with the help of Dr. Harthoorn. The radiotracking equipment was designed and constructed by Dr. Howard Baldwin of Sensory Systems Laboratories, Tucson, Arizona. In the later versions the equipment gave a range of 50 km initially, and lasted for about four months. The transmitters were embedded in fiberglass, shaped to sit comfortably on the back of an elephant’s neck, and attached to a collar of 3 1/2” machine belting which was counterweighted at the bottom with a piece of lead so that the transmitter should remain on top. The receiving equipment could be mounted on the struts of an aeroplane, or on a car, or carried on foot, thus providing maximum operational flexibility.

The movements were recorded by measuring the straight line distances between radio fixes made at specific time intervals. On the occasions when the actual meandering courses were continuously plotted, they were found to exceed the straight line values by a considerable margin. Nevertheless, it was impractical to employ continuous tracking for all the groups and for the purpose of comparing one set of observations with another, the straight line values provided a satisfactory record.

In all cases but one, the individuals radiotracked were members of family units. From direct observations of these individuals and from other data on the social behaviour of elephants (Douglas-Hamilton, 1966, 1967, 1969 and in preparation), it is considered that the movements of each individual were identical to those of the family to which it belonged.

Results

24 hourly movements

All animals from the three study areas were plotted at 24 hourly intervals thus allowing comparisons to be made between Manyara, Tarangire and Serengeti. The shortest change of position of any elephant over 24 hours was 0.2 Km and the longest was over 30 km. Within this span the mean movements of different individuals varied significantly.

The results summarized in Table I (see end of text) show that the Manyara elephants moved the least with a mean 24 hourly change of position that varied between 1.9 and 2.9 km. In contrast, the Tarangire family moved on average 5.7 km/2 hours and the Serengeti family 21.4 km/24 hours.

The range sizes increased in the same way. They were determined by measuring the area enclosed by a line joining the outside position records. The Manyara elephants utilized between 23 Km^2 and 52 Km^2 while the Tarangire group had a range of 330 km . It was impossible to estimate the area of the Serengeti elephants' range as there were too few observations, but if the longest axis across a range is used as a measure of its size, then the Serengeti elephant had the largest range, with a long axis of more than 64 kin, compared to 30 km for Tarangire and between 15 and 26 km for Manyara.

The probable explanation for these variations in movements and range sizes are as follows. The Manyara elephants live in an area of high primary productivity with an abundant food supply, including a forest that is irrigated all round the year by a series of springs. There is a wide diversity of habitat types all easily accessible and in close proximity of each other within the relatively small area of the National Park. Elephants do not have to move far between the escarpment, the forest, the swamp, the *Acacia tortilis* woodlands and the rich alkaline pastures. The advantages to animals of frequenting the boundary zones between habitat types has been described by Lamprey (1963) and Manyara is exceptionally well endowed with these. In contrast, Tarangire is a much more arid environment with vegetation types whose boundaries are spread far apart. Yet even here Lamprey found that elephants tended to frequent the boundary zones. It is likely that to maintain a sufficiently varied diet and even to get from the river to their feeding areas, the Tarangire elephants are forced to move much greater distances and to cover a much larger total area than their Manyara counterparts.

An additional factor restricting the Manyara population is the growth of the surrounding human populations which has displaced them and which now confines them within less than half their former range (Douglas-Hamilton 1969). Yet surprisingly no single bull or family unit at Manyara utilized the entire area at its disposal, although the population as a whole did. This self imposed restriction and the high fertility and good condition of the Manyara elephants lead to the conclusion that their movements are mainly governed by their nutritional needs and that they have no reason to move more than 3 - 5 km/24 hours. The effect of human influence on their movements is discussed later.

The Serengeti movements are large for a different reason. The sample was only drawn from a short period when the elephants were extremely disturbed. The population from which the experimental animal was taken is known to be very nervous. It appears that the disturbances caused by the immobilization and the subsequent aerial radio locations caused the elephants to move abnormally fast and in a consistent direction away from the scene of the darting. Unfortunately the transmitter failed after four days and all further information was lost, but even in this short time, the distance across their range suggested that their total range had the highest value of the three different areas. Why it should be higher than that of the Tarangire elephant remains a matter for speculation. Only further long term observations can resolve this question (Croze work in progress)

Daily and nightly movements in Manyara

In Manyara it was possible to make much more detailed observations, and these animals were plotted either continuously or at 12 hourly intervals, usually at dawn or dusk so that the daily and nightly distances covered could be recorded. The straight line daily movements of the elephants varied between 0.2 and 8.2 km, and the nightly movements between 0.4 and 3.5 km. The values summarized in Table I show significant differences between individuals in the mean daily and nightly movements. Family 7 had approximately the same mean daily movements as M9, but both were significantly greater than those of F16. The movements by night of F16 and F7 were similar but both were greater than the nightly movements of M9. These tendencies are summarized in Table 2. The differences here have been tested by the median test (Siegel 1956) and found to be significant.

Table 2

DAY MOVEMENT	“TAME” F7	$\bumpeq$	“TAME” M9	>	“WILD” F16
NIGHT MOVEMENT	“WILD” F16	$\bumpeq$	“TAME” F7	>	“TAME” M9

A possible explanation for the daily differences between the groups is that the members of Family 16 were extremely nervous elephants, much wilder than those of Family 7 or Male 9. Consequently they tended to hide during the day, by lying up in dense thickets and keeping far away from the tourist roads. In fact it was only possible to plot their movements by radio locations made from the aeroplanes. By avoiding the extensive road networks, their movements became very restricted. In contrast, Family 7 and Male 9 were thoroughly habituated to the presence of motor cars and would pass within 20 yards of them without showing signs of disturbance. By night, however, the "wild" Family 16 was free of all traffic and tended to move more than it did by day, although not more than the "tame" Family 7.

As a result of radiotracking it was possible to improve the range maps made from standard ground observations for the three groups at Manyara. The new maps showed that although the elephants kept mainly within the Park they did occasionally venture outside. This data is of great significance to the National Park's management. The maps also showed that even though they were hemmed in by human settlement on three sides and by a lake on the fourth side, the elephants did not use all the land that was available to them.

Summary

The sizes of daily movements and ranges of elephants are described for five different individuals in three different areas. It has been shown that the movements and ranges vary greatly not only from area to area but also from one individual to another. It seems likely that the factors controlling these differences are related to the nutritional requirements and "wildness" or "tameness" of the individuals concerned.

Although observations made in Manyara and Tarangire supported the idea that elephant movements are small compared to previous estimates, the Serengeti record revives the possibility that some elephants do cover very large distances.

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Table 1

	MEAN VALUES				RANGE				
	12 Hour day movement	12 Hour night movement	24 Hour day + night movement	24 Hour straight movement	Longest axis	Area	No. of position records	Period of study	Season
MANYARA									
“Tame” Family 7	2.7 km	1.7 km	4.4 km	2.9 km	26	52 km^2	184	127 days	wet & dry
“Wild” Family 16	1.2 km	1.6 km	2.8 km	1.9 km	19.5	42 km^2	64	110 days	wet & dry
“Tame” male 9 Food very abundant	2.5 km	0.9 km	3.4 km	2.5 km	15	23 km^2	35	18 days	dry
TARANGIRE									
“Wild” Family 1 Food scarce	-	-	-	5.7 km	30	330 km^2	24	61 days	wet & dry
SERENGETI									
“Very wild” Family 1 Food abundant	-	-	-	21.4 km	64 km across	-	4	4 days	wet

Appendix 8.1 Inter-family unit association matrix: January 1966 - June 1970

Each cell contains the number of times that two family units were seen less 1 km apart.

HEC 2	ANI 3	ATD 4	APH 5	ARI 6	BOA 7	JEZ 8	LEO 9	CAT 10	JAG 11	HEL 12	CLY 13	DTR 14	DEI 15	JEY 16	GRZ 17	JOC 18	MAR 19	LED 20	OLD 21	OPH 22	ORI 23	SAR 24	RHE 25	POR 26	SPH 27	TEC 28	MRS 29	ANT 30	VIC 31	FLO 32	GAP 33	TOR 34	GON 35	SHE 36	GRA 37	PRU 38	BAL 39	ASS 40	ISA 41	JEY2 42	DPV 43	CRS 44	JUD 45	MYST 46	JEY3 47	Family uniy	Alone	Total associations	Times seen	% Alone
30	14	3	2	9	17	22	11	22	13	20	4	7	7	3		12	12	9	7	4		20	12	17	21	4		3	17	21	1							11	5							AET 1	24	360	107	22
	7	1		5	17	16	10	11	12	13	1	4	4	2		8	3	2	9	4		9	6	13	14	3		2	13	14								10	7							HEC 2	5	250	54	9
		8	1	17	24	25	22	18	8	8	2	4	8	3		19	9	6	17	13	1	16	22	27	31	1			25	21		1						15	8	1			1			ANI 3	39	403	130	30
			3	8	10	4	7	3	2	1	2	11	3	2		7	4		7	10	3	2	6	4	8	3	2	2	13	8								6	2	1						ATD 4	16	156	58	28
				2	2	2	1	1	1	1	1	4				2				1	2	2	3	1	2				4	5		1						2	2							APH 5	53	48	73	71
					34	30	31	18	11	14	4	8	8	1		24	7	4	16	7	3	22	22	31	34	9	3	7	32	30		3		1				23	12	1			3			ARI 6	56	494	186	30
						64	170	46	15	30	6	8	13	2		21	19	11	25	10	1	42	31	57	49	9	4	8	56	50	2	2		1				39	102					1		BOA 7	43	1098	314	14
							129	39	16	29	5	5	19	4		24	21	14	21	6		39	33	56	50	7	2	5	63	46	1	1		1				41	69					1		JEZ 8	31	1010	262	12
								36	10	20	5	5	10	4		17	17	8	16	5		31	26	41	39	10	6	8	42	37	1	1		1				30	71	1				1		LEO 9	11	880	210	5
									32	53	6		9	6		11	6	5	20	4		31	18	37	26	8	1	4	27	32	3	1						22	17	1			1	2		CAT 10	27	577	153	18
										34	1	3	5	1		8	4	3	11	4	1	9	13	13	11				12	16								8	9							JAG 11	10	286	74	14
											2	1	9	5		11	5	6	15	3		19	11	27	26	3		1	19	27								15	12					3		HEL 12	11	443	112	9
												1	4	5	1	5	1	2	3	1		5	6	3	8	9	4	11	2	4	2	2		1	1		2	2	4	3		1		2	3	CLY 13	10	137	38	26
													1			5	6	5	2	12	3	6	8	4	6	1	1	1	6	6	6	3												1		DTR 14	29	144	79	37
														3		10	2	2	10	5	1	16	6	11	21	4	5	12	17			1				1		6	7						1	DEI 15	12	239	63	19
															1	9	3	3	4			5	2	2	5	5	1	4	4	4	2				1	1		3	1	19				1	21	JEY 16	16	142	65	24
																															1					2	2			1	1			1	1	GRZ 17	5	11	11	45
																	9	3	21	12	1	23	12	32	26	4	1	5	28	27	1	2		2				18	8	1			2	1		JOC 18	41	432	154	26
																		32	9	4	1	14	4	11	15		1		11	5				1				9	6	1					1	MAR 19	4	253	66	6
																			3	1	1	8	3	8	11	1	2	2	9	5				1				5	2							LED 20	1	177	43	3
																				4		25	16	30	33	5	3	6	26	29		2						13	9	1			2	1		OLD 21	15	421	98	15
																					2	5	5	6	8			2	12	11		2						15	3							OPH 22	32	181	89	35
																									1				2	2																ORI 23	15	25	23	54
																							28	86	40	4	1	3	36	34	2					2		50	18							SAR 24	15	653	163	9
																								31	29	6	2	4	32	34	2							28	15				1	1		RHE 25	18	478	122	15
																									43	6	2	2	55	55	2	3				1		90	22				1			POR 26	9	830	211	4
																										9	4	6	56	56		2						29	18	1				3		SPH 27	44	741	214	20
																											10	24	7	9	1	2				2		3	6	2				1		TEC 28	5	179	46	11
																												9	3	2								1	1	1				2	1	MRS 29	0	70	13	0
																													7	7		2				1		1	4	1				1	1	ANT 30	1	147	34	3
																														144	1	4		1				27	22	3					1	VIC 31	49	833	281	17
																															3							35	22	1			2	1		FLO 32	23	822	234	10
																																				2			1	1				3		GAP 33	2	30	12	17
																																						1							1	TOR 34	3	36	10	30
																																														GON 35				
																																							1							SHE 36	2	11	6	33
																																												2		GRA 37	1	4	4	25
																																					1	1							1	PRU 38	3	15	13	23
																																								1						BAL 39	0	6	4	0
																																						21	1					1	1	ASS 40	22	589	167	17
																																														ISA 41	6	510	115	5
																																												1	14	JEY2 42	0	54	23	0
																																								1						DFV 43	1	4	3	33
																																														CRS 44	0	1	1	0
																																														JUD 45	0	16	6	0
																																														MYST 46	9	31	25	36
																																														JEY3 47	0	47	27	0
																																														TOTAL		14,274	4,197	

Appendix 8.2

OBSERVED AND EXPECTED ASSOCIATION VALUES FOR SELECTED FAMILY UNITS

This table summarizes the number of associations observed each year between family units which are found to be significantly associated at the .01 probabilty level in the summed 4 $^1/_2$ years of data. An expected value has been calculated for each cell by the formula described in chapter 5.

Associated family units		1966	1967	1968	1969	1970	Total 66-70	$\frac{O^x - E}{\sqrt{E}}$ 66-70	Probability < .01	< .001
AET - HEC	Obs.	0	0	16	8	6	30	4.28	+	+
	Ex.	0.07	0.48	3.7	1.36	1.27	6.44			
HEC - JAG	Obs.	0	1	7	4	0	12	3.05	+	
	Ex.	0.09	0.5	4.4	0.54	0.34	5.11			
ANI - OPH	Obs.	0	2	8	3	0	13	3.41	+	+
	Ex.	0.08	1.4	1.6	1.7	0.22	5.22			
ATD - DTR	Obs.	0	2	5	3	1	11	7.46	+	+
	Ex.	0	0.2	1	0.59	0.08	1.59			
ATD - OPH	Obs.	0	2	4	3	1	10	5.65	+	+
	Ex.	0	0.5	1.2	0.67	0.04	2.00			
APH - DTR	Obs.	0	0	1	2	1	4	5.03	+	+
	Ex.	0.08	0.14	0.1	0.09	0.01	0.49			
DTR - OPH	Obs.	0	3	5	3	1	12	7.47	+	+
	Ex.	0.01	0.4	0.95	0.59	0.04	1.85			
BOA - JEZ	Obs.	11	31	43	69	10	164	8.75	+	+
	Ex.	5.5	15.5	27.54	37.64	3.19	83.89			
BOA - LEO	Obs.	20	27	45	69	9	170	11.41		
	Ext.	4.7	12.5	25.02	32.55	2.81	72.74			
BOA - ISA	Obs.	0	22	31	41	8	102	9.37	+	+
	Ex.	0	8.2	15.8	20.47	1.07	41.59			
JEZ - LEO	Obs.	8	20	38	53	10	129	7.63	+	+
	Ex.	3.8	11.6	23.4	27.8	3.49	66.68			
JEZ - ISA	Obs.	0	15	24	28	2	69	5.00	+	+
	Ex.	0	7.6	14.7	17.48	1.33	38.13			
LEO - ISA	Obs.	0	13	25	28	5	71	6.60	+	+
	Ex.	0	6.2	13.7	15.12	1.17	33.06			
CAT - JAG	Obs.	6	5	14	4	3	32	5.82	+	+
	Ex.	0.07	0.48	3.7	1.36	1.27	6.44			
CAT - HEL	Obs.	7	9	21	11	5	53	7.99	+	+
	Ex.	2	2.3	8.93	5.57	0.58	18.57			

Appendix 8.2 (continued).

Associated family units		1966	1967	1968	1969	1970	Total 66-70	$\frac{O^{x} - E}{\sqrt{E}}$	Probability < .01	< .001
JAG - HEL	Obs.	3	3	20	5	3	34	8.25	+	+
	Ex.	1.2	0.7	7.98	1.27	0.15	9.11			
JOC - OPH	Obs.	0	2	7	2	1	12	2.71	+	
	Ex.	0.02	2	1.68	1.16	0.42	5.6			
MAR - LED	Obs.	0	2	8	11	11	32	16.15	+	+
	Ex.	0.01	0.04	0.8	1.13	2.03	3.19			
OPH - ASS	Obs.	1	6	7	1	0	15	2.64	+	
	Ex.	0.	4.2	1.81	2.07	0.04	7.68			
SAR - POR	Obs.	2	19	28	21	16	86	7.26	+	+
	Ex.	2.2	12.2	12.73	7.09	6.98	40.05			
SAR - ASS	Obs.	4	11	11	15	9	50	4.11	+	+
	Ex.	2.8	10.8	5.63	6.13	3.79	28.17			
POR - ASS	Obs.	11	39	12	18	10	90	8.99	+	+
	Ex.	2.8	19.8	6.37	7.37	4.33	36.04			
VIC - FLO	Obs.	28	29	31	38	18	144	13.04	+	+
	Ex.	11.9	6.9	13.4	13.4	7.54	50.92			
JEY1 - JEY2	Obs.	0	1	5	0	13	19	25.1	+	+
	Ex.	0	0.02	0.04	0	1.54	0.54			
JEY1 - JEY3	Obs.	1	4	5	2	9	21	29.92	+	+
	Ex.	0.01	0.1	0.04	0.01	0.86	0.47			
JEY2 - JEY3	Obs.	0	0	5	1	8	14	32.72	+	+
	Ex.	0	0.01	0.04	0	0.32	0.18			
CLY - TEC	Obs.	0	1	2	3	3	9	5.51	+	+
	Ex.	0	0.1	0.37	0.55	1.23	1.74			
CLY - MRS	Obs.	0	0	3	0	1	4	4.04	+	+
	Ex.	0	0	0.39	0.07	0.2	0.68			
CLY - ANT	Obs.	0	0	3	3	5	11	8.02	+	+
	Ex.	0.01	0.03	0.39	0.2	1.44	1.43			
TEC - MRS	Obs.	0	0	7	1	2	10	9.69	+	+
	Ex.	0	0	0.57	0.12	0.22	0.89			
TEC - ANT	Obs.	0	3	9	4	8	24	16.21	+	+
	Ex.	0	0.04	0.57	0.33	1.59	1.87			
MRS - ANT	Obs.	0	0	7	0	2	9	9.71	+	+
	Ex.	0	0	0.59	0.04	0.26	0.73			

Appendix 8.3

Inter-family association by X^2 analysts.

The basic feature of this method is the 2 x 2 contingency table (Southwood, 1966).

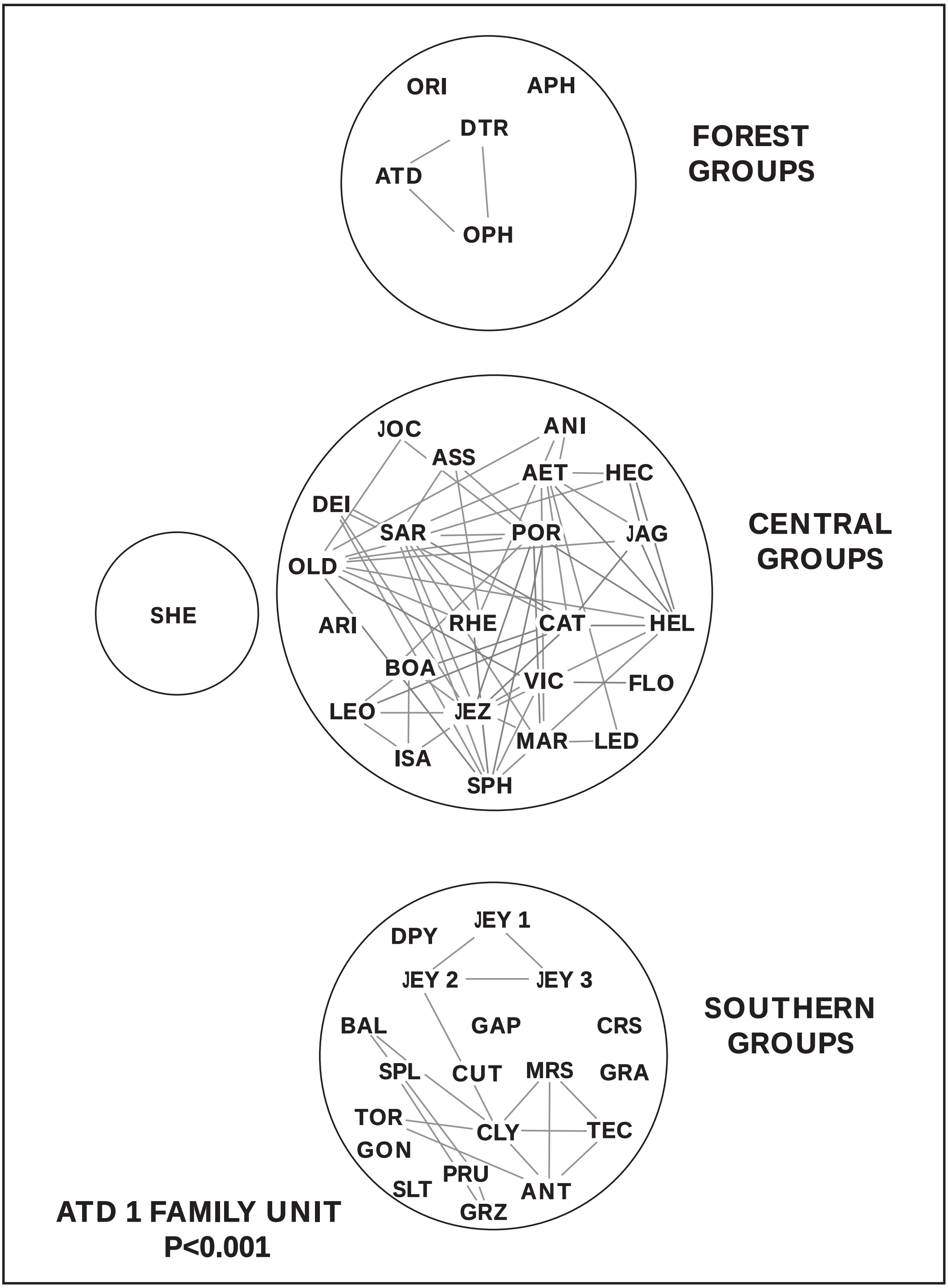
Family Unit A	**Family Unit B**		
	Present	**Absent**	
Present	a	b	a + b
Absent	c	d	c + d
	a + c	b + d	n = a + b + c + d

A corrected X^2 is calculated for unit association matrix (Appendix 8.1).

Unlike the method of analysis described in Chapter 5 this test includes all occasions in which single family units were observed alone. All association at the .001 P level between family units are indicated in the figure opposite, which follows the same format as Fig. 5.16 explained on p.84. The web of associations seen amongst the central groups may correspond to a ‘clan’ level of organization, but could merely be an artefact of shared home range.

Figure 8.3

Inter-family associations by X^2 analysis.



APPENDIX 9

MANYARA PLANTS EATEN BY ELEPHANTS.

ACANTHACAEAE
Asystasia gangetica
Blepharis maderaspatensis
Ecbolium revolutum
Hypoestes verticillaris
Justicia betonica
J. glabra
J. heterocarpa
J. nyassana
J. striata
Peristophe bicalyculata

AI ZOACEAE
Zaleya pentadra

AMARANTHACEAE
Aerva lanata
Amaranthus dubius
Aschyranthus aspera
Digera muricata
Sericomopsis hildebrantii

AMPELIDACEAE
Cissus quadrangularis

ANACARDIACEAE
Lannea stuhlmannii
Sclerocarya birrea

APOCYANACEAE
Conopharyngea usambarensis
Rauvolfia caffra

BALARITACEAE
Balanites aegyptiaca

BIGNONACEAE
Kigelia africana

BOMBACACE AE
Adansonia digitata

BORAGINACEAE
Cordia goetzii
C. ovalis
C. rothii

BURSERACEAE
Commiphora baluensis

CAESALPINACEAE
Delonix elata
Tamarindus indica

COMBRETACEAE

Tenrninalia brownii

COMMELINACEAE

Commelina benghalensis
C. foliacea

COHPOSITAE
Pluchea dioscorides
Veronia cinerascens

CAPPARIDACEAE
Capparis fasicularis
Maerua triphylla
Thylachium africanum

CONVOLVULACEAE
Ipomoea obscura

CUCURBITACEAE
Cucumis dipsaceus
Lageneria sphaerica

CYPERACEAE
Cyperus alternifolius
C. articulatus
C. rotundus
Kyllinga controversus

EBENACEAE
Diospyros abyssinica

EUPHORBIACEAE
Acalypha fruticosa
Bridelia micrantha
Croton macrostachys
C. megalocarpa
Phyllanthus maderaspatensis
P. sepialis
Ricinus communis

FLACOURTIACEAE
Dovyalis zanthocarpa

GRAMINAE
Bothrlchloa insculpta
Brachiaria deflexa
Cenchrus ciliaris
Chloris gayana
C. pycnothrix
Cynodon dactylon
C. plectostachyus
Dactyloctenium aegyptium
Digiteria milanjiana
Echinochloa haploclada
E. pyramidalis
Enteropogon macrostachyus
Eragrostis aethiopica
Panicum deustrum
P. maximum
Panicum meyrianum
Pennisetum merianum
Setaria plicatilis
S. sphacelata
Sporobolus consimilis
S. marginatus
S. pyramidalis
S. spicatus
Tetrapogon tenellus
Urochloa trichopus

GUTTI FERAE
Garcinia livingstonei

LABIATAE
Becium sp.
Leucas glabrata
Ocimum suave

MALVACEAE
Abutilon mauritanium
Hibiscus micranthus
H. palmatus
H. vitifolius
Pavonia patens
Sida ovata
S. rhombifolia

MELIACEAE
Ekebergia buchananii
Trichilea roka

MIMOSACEAE
Acacla albida
A. brevispicata
A. clavigera
A. etbaica
A. mellifera
A. sieberiana
A. tortilis
A. xanthophloea
Albizia anthelminthica

MORACEAE
Antiaris toxicaria
Ficus sycamorus

NYCTAGINACEAE
Boerhaavia coccinea

OLACACEAE
Ximenia Americana

PALMAE
Hyphaenae sp.
Phoenix reclinata

PAPILIONACEAE
Clitoria ternatea
Dalbergia melanoxylon
Indigofera arrecta
I. costata
I. schimperi
I. tectoria
Lonchocarpus bussei
Rhynchosia sp.
Sesbania sesbans
Tephrosia villosa
Vigna milotica

POLYGONACEAE
Oxygonum sinuatum

RHAMNACEAE
Ziziphus pubescens

RUBIACEAE
Gardenia jovis-tonantis
Vangueria acutiloba

RUTACEAF
Fagara calybea

SALVADORACEAE
Salvadora persica

SAPI NDACEAE
Zanha golungensis

SOLANACEAE
Solanum icanum
Stictocardia incomta

STERCULIACEAE
Sterculia stenocarpa

TILIACEAF
Grewia tembensis
G. villosa

TYPHACEAE
Typha angusti folia

ULMACEAE
Celtis africana
C. zenkeri

VERBENACEAE
Priva cordifolia

ZYGOPHYLLACEAE
Tribulus terrestris

Appendix 10

Elephant densities in Africa.

Area	Date	Sample atrea		Mean	Mean density		Source	Method and comments
		M/^{2}	Km^2	No.	E/m/$^{2.}$	E/Km^2.		
TANZANIA								
Manyara N.P.	1961	440	103.2	400	10	3.9	Morgan Davies (1961)	Ground estimate
	1965	33	85	420	14	5	Watson & Turner(1975)	Aerial count
	1966-1970	33	85	427	14	5	This study	Aerial counts
Serengeti N.P. (North and South)	1962-65 1965				0.78 0.27	0.263 0.104	Watson and Bell (1969)	Occupance flights
	1965)			2092			Lamprey et. al. (1969)	Aerial and photographic counts
	1966)			2209			“ “	counts
	1967)			1961				
	1969)	3800	9804	2200	0.6	0.23	Croze (pers.comm.)	Aerial counts
Ruaha N.P. (inner bank)	1967	160	412.8		2.8 1.6-8.3	1.1	Savidge (1968)	Aerial counts
	1969	3876	1x10^4	20000	5.2	2	Hendrichs (1971)	Rough estimate
Ngurdoto Crater N.P.	1967	7	18.6	60	8,5	3.3	Vesey-Fitzgerald (1968)	Ground estimate

Appendix 10 (continued)

Area	Date	Sample atrea		Mean	Mean density		Source	Method and comments
		M/²	Km²	No.	E/m/².	E/Km².		
Arusha N.P. (including above)	1970	42	108.4	160-200	3.8-4.8 1.86	1.47	Vesey-Fitzgerald (pers. Comm)	Ground estimate
Mikumi N.P.	1970	450	1161.0	300-500	0.67-1.1	0.26-0.43	S. Stephens (pers. comm.)	Ground estimate
Mkomazi G.R.	1969	4.2	10357		2.1 (16.8-2.8)	0.82 (6.5-1.1)	Watson et. al. (1969)	Random aerial counts
Yaida Chini G.R.		1000	2580	1000	1	0.39	P. Enderlein (pers. Comm.)	Rough estimate from aerial count*
Ngorongoro Crater C.A.		102	263.2	28	0.274	0.11	Turner & Watson (1964)	Aerial count
Eastern Sealous G.R.	1967-69	750	1935.0	800-1000	1.1-1.3	0.43-0.50	W.A. Rodgers (pers. (comm..)	Unspecified
KENYA								
Tsavo N.P.	1968				1.2 1.33	0.46 0.51	Laws (1969b) Laws (in press)	Aerial counts
Marsabit N.P.	1970	320	825.6	300	1.0	0.39	P. Jekins (pers.comm.)	Rough ground Estimate*

Appendix 10 (continued)

Area	Date	Sample atrea		Mean	Mean density		Source	Method and comments
		M/^{2}	Km^{2}	No.	E/m/$^{2.}$	E/Km^{2}.		
Arberdares N.P.	1970			500-700			B.Woodley (pers. Comm.)	Rough ground estimate*
Meru N. P.	1970	380	980.4	600-800	1.6-2.1	0.62-0.81	P. Henkions (pers. Comm.)	Aerial counts*
UGANDA								
North Bunyoro Area	1966-67				7.7	2.9	Laws et al (1970)	Aerial counts
					4.9	1.9-3.8	laws (in press)	Aerial counts (two density strata)
Queen Elizabeth N.P.	1963-67				0.15-9.1	0.06-3.51	Field &Laws (1970)	Ground transect counts (10 sample areas)
	1966-69			3900	6.4	2.5	Field (1971)	Aerial counts
Kidepo Valley N.P.		500	1290	850	1.7	0.66	1. Ross (pers. Comm.)	Sample aerial counts
ZAMBIA								
Loangwa valley	1966			23600.1	2.3 (1.3-3.6)	0.9 (0.5-1.4)	Dodds & Patton	Aerial transect count

APPENDIX 10 (Continued)

Area	Date	Sample Area		Mean	Mean density		Source	Method and comments
		M/^{2}	Km^2	No.	E/m/$^{2.}$	E/Km^2.		
Chfungwa plain	1965	64	165.1	1141	17.8	0.69	Dodds & Patton (1968)	(Total aerial (counts (reliability unknown)
Lundu plain	1965	15	38.7	492	32.8	12.7	“ “	
Zambezi valley	1969-70	72,300	5934	4235	1.9	0.74	W.C.I. Brochure (1972)	
RHODESIA								
Kariba area	1964-67				15.0	5.8	Jarman (1971)	Ground transects
MALAWI								
Kasungu G.R.	1969	800	2064	650	0.8	0.31	R.P. Zimmerman (pers. Comm..)	Ground estimate*
SOUTH AFRICA								
Kruger N.P.	1966	7360	928.8	2374	0.32	0.12	Pienaar (1966)	One total aerial Count
Addo N.P.	1919	100	258	138	1.38	0.53	Archibald (1954)	
	1935	26	67	23	.9	0.4	“ “	
	1955	26	67	18	0.7	0.3	“	

* These data are from personal communications in answer to a questionnaire sent out by Dr. H. Croze and myself.

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Agenda

*1. Cooper, C.F. (1963). An evaluation of variable plot sampling in shrub and herbaceous vegetation, Ecology 44: 565-568

*2. Craighead, F.C. Jr. and Craighead, J.J. (1963). Proc. 18th Ann. Instr. Soc. Amer. Conf. Biotelemetric Session.

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