Seasonal Movements, Migration and Age Determination of Burchell's Zebra (*Equus burchelli antiquorum*, H. Smith, 1841) in the Kruger National Park

By

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Submitted in partial fulfilment of the

requirements for the degree of

Master of Science

in the

Faculty of Science,

University of Pretoria,

Pretoria.

November, 1972

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Chapter 1.

INTRODUCTION

Due to its adaptive flexibility, Burchell's zebra (*Equus burchelli antiquorum*, H. Smith, 1841) still enjoys a wide distribution in Southern Africa. Although largely confined to game reserves and private game farms, its numerical status is good and leaves no cause for concern. In the Kruger National Park it is the third most abundant large mammal species, after the impala (*Aepyceros melampus*) and the buffalo (*Syncerus caffer*).

Because of variations in the stripe pattern of the different species and subspecies, and even within a subspecies, zebra have never failed to intrigue taxonomists. In addition to this, popularity of the zebra as a game animal stems from the economic and trophy value of its skin, its meat as a source of protein, the early attempts at its domestication and last but not least its general abundance and decorative value (Stevenson-Hamilton, 1925).

1.1. Nature of the problem.

Since the appointment of the first Warden in the Sabi Game Reserve (which included a large tract of land between the Crocodile and Olifants rivers outside the present western boundary of the Park) in 1902, there has been a steady increase in the growth curve of the zebra population. This tendency, with a few exceptions, has been typical for most of the Park's large ungulate species. The addition of the Shingwidzi Game Reserve (area between the Groot Letaba and Levubu rivers) in 1903 and the proclamation of the Kruger National

Park in 1926, together with associated game management practices such as fire control, reduced poaching and hunting, disease and predator control and water provision, resulted in a predictable population explosion - large tracts of prime game habitat previously being almost devoid of big game animals. Despite a series of droughts after 1926, mild culling and outbreaks of anthrax in 1959, 1961 (Pienaar, 1960; Pienaar, 1961) and 1970, the ungulate population of the Park, especially elephant (*Loxodonta africana*), buffalo, impala, zebra and wildebeest (*Connochaetes taurinus*) have continued to increase.

1.2. Purpose of the investigation.

The increase in numbers of certain large mammal species associated with a parallel decrease in the growth curves of others, together with the effect which these species have on the habitat (vegetation, water and soil) resulted in the instigation of a number of research projects of a geological, botanical and zoological nature. It is hoped that the data eventually assembled will ensure that the management practices adopted in the Kruger National Park are based on sound scientific facts.

With regard to the zebra project, initial research has been concentrated on age determination and general behaviour with the simultaneous collection of data on reproduction and population dynamics. These last mentioned subjects will be dealt with in a later publication.

1.3. Most significant outcome of the investigation.

Since the initiation of this project in January 1969, it has been possible to develop a very practical and accurate method of ageing zebra. The validity of the technique, based on the eruption,

replacement..../- 3 -

replacement and wear of the incisors, premolars and molars, has been aptly substantiated by the discovery of annual rings in the cementum of certain of the teeth.

By utilizing resightings on 141 marked zebra it has been possible to trace their seasonal and migratory patterns and gain a knowledge of the factors determining their distribution, choice of habitat and home range size. This data has also indicated that the zebra population of the Kruger Park can be divided into a number of fairly discrete units or sub-populations. This information will assist with the allocation of culling quotas to the individual units, and an understanding of the population regulating mechanisms operating in the different units.

1.4. Particulars in connection with the study area.

For administrative purposes the Kruger National Park is divided into three districts:

(i) The northern district - area north of the Olifants river,

(ii) the central district - area between the Olifants and Sabie rivers,

(iii) the southern district - area south of the Sabie river.

Before discussing the effects of vegetation, climate, physiography, geology, fire and biotic factors on the distribution and movements of zebra, it is essential to describe the local conditions in some detail.

1.4.1. Physiography and geology.

Topographically the Kruger Park is rather interesting, since,

although..../- 4 -

although appearing rather flat, it in fact presents an undulating landscape interrupted at intervals by deep seasonal or perennial water courses and rocky outcrops or koppies. There are no true mountain ranges in the Park, but the Lebombo ridge on the eastern boundary, the Malelane area and the area north of Punda Milia may be described as mountainous (Pienaar, 1963). Just west of the Lebombo ridge the country tends to be rather flat, in contrast to the western half of the Park, and is consequently known as the Lebombo flats. The highest altitudes are attained in the south-west (835 metres above sea level). Towards the east there is a gradual decline, with the Lebombo flats only some 180-240 metres above sea level.

The Park, which encompasses an area of some 1901119 hectares, is bordered on its north and south by the Limpopo and Crocodile rivers respectively. The eastern boundary is also natural being formed to a large extent by the Lebombo mountain range. On the west the boundary is formed by some 480 kilometres of barbed-wire fence. This fence, completed early in 1961, was erected for various reasons, the most important being to control the spreading of foot-and-mouth disease between animals within the Park and private domestic stock to its west. All these boundaries are to a greater or lesser extent important faunal barriers, elephant being the only animals to cross all the boundaries fairly regularly. The effect which boundaries have on the movements of zebra will be discussed in chapter 4.

The Park, which actually lies between the Drakensberg escarpment and the Indian ocean,)between latitude 22°25' to 25°32' south and longitude 30°50' to 32°2' east), is drained by two major river systems (Pienaar, 1968b) - the Limpopo and the Incomati. Each of these major systems are fed by a number of sub-systems (primarily perennial) which are in turn fed by several important seasonal tributaries. The sub-systems of the Limpopo from north to south are:

(i) the Levubu-perennial
(ii) the Shingwidzi - seasonal
(iii) the Groot Letaba - perennial in the past, but now seasonal
(iv) the Olifants - perennial.

The sub-systems of the Incomati from north to south are:

(i) the Nwanetzi - seasonal
(ii) the Nwaswitsontso - seasonal
(iii) the Sabi - perennial
(iv) the Crocodile - perennial.

Although regarded as perennial, the Letaba, Levubu and Crocodile rivers may stop flowing for short periods during dry years.

The Limpopo river and its sub-systems, as well as those of the Incomati, pass through the Park in a west-east direction. The seasonal rivers usually only flow for a short time during the rainy summer months, but form important drinking sites due to a series of semi-permanent and permanent pools along their length. The perennial rivers are important and often stringent faunal barriers, especially during the summer months when they may be in flood. During the dry season, however, most medium-sized and large game can cross without difficulty.

The geology of the Park has been discussed in some detail by Van der Schijff (1957), while Pienaar (1966a) in his publication "The Reptiles of the Kruger National Park" gives a useful geological

map of..../- 6 -

map of the area. For the purpose of this study the geological maps provided by the above authors have been combined and simplified as illustrated in Fig. 1.1.

1.4.2. Climate.

Webster (1954) defines climate as "the average course or condition of the weather at a particular place, over a period of many years".

Since the data discussed in this treatise were collected mainly during 1969, 1970 and 1971, only the corresponding weather conditions will be analysed and compared to the norm.

1.4.2.1. Precipitation.

In the Kruger National Park rainfall is in the form of thundershowers which may occasionally be accompanied by lightning and hail. More than 80% of the rain falls during the summer months (October to March); almost rainless periods of up to three months are common. The mean annual rainfall varies from about 390 mm in the extreme north-east at Pafuri to 706 mm in the south-west around Pretoriuskop. There is thus an increase in the mean annual precipitation from north to south. The mean annual rainfall for 12 different stations in the Park is given in Table 1.1. (Brynard, 1964).

Table 1.1...../- 7 -

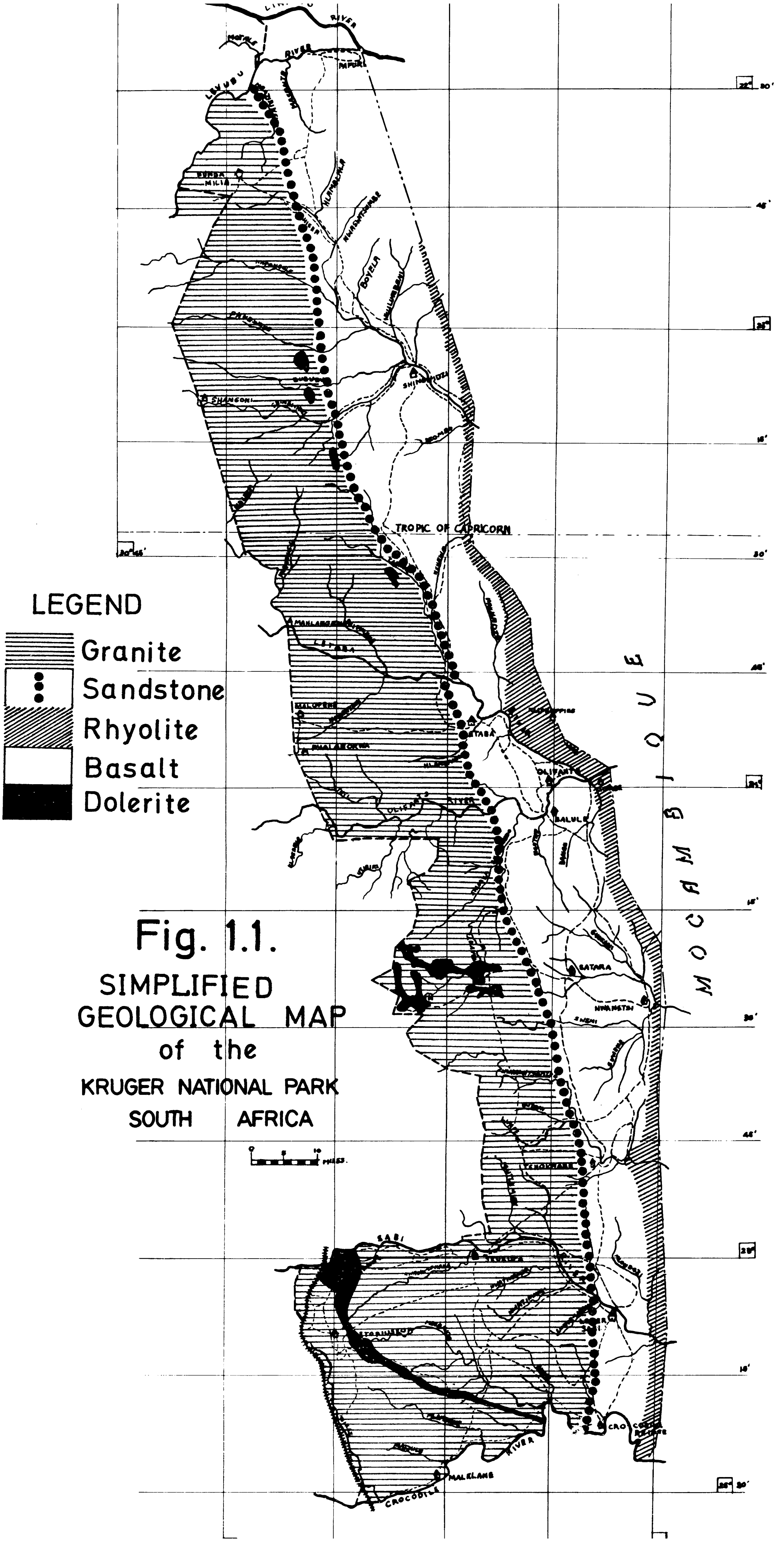


Fig. 1.1.
SIMPLIFIED
GEOLOGICAL MAP
of the
KRUGER NATIONAL PARK
SOUTH AFRICA

Table 1.1.

Mean annual rainfall for 12 different weather stations in the Kruger National Park

Station	No of years covered	Average rainfall mm
Pretoriuskop	20	706,09
Malelane	19	604,27
Crocodile Bridge	20	621,28
Tshokwane	21	587,76
Satara	25	550,16
Letaba	26	427,74
Shingwidzi	23	435,61
Punda Milia	26	528,07
Shangoni	17	569,72
Kingfisherspruit	2	676,40
Pafuri	21	398,27
Skukuza	43	570,99

Since rain is an important factor in determining the migratory behaviour of zebra in the central district, the mean monthly precipitation calculated from four weather stations in this area has been plotted for 1969, 1970 and 1971 (Fig. 1.2.).

1.4.2.2. Wind.

The mean wind direction determined at Skukuza over a two year period (1970 and 1971) from three daily readings, indicates that the prevailing winds blow from a south-easterly and a southerly direction.

The amount of wind from the various compass directions may be broken down as follows:

south-east..../- 8 -

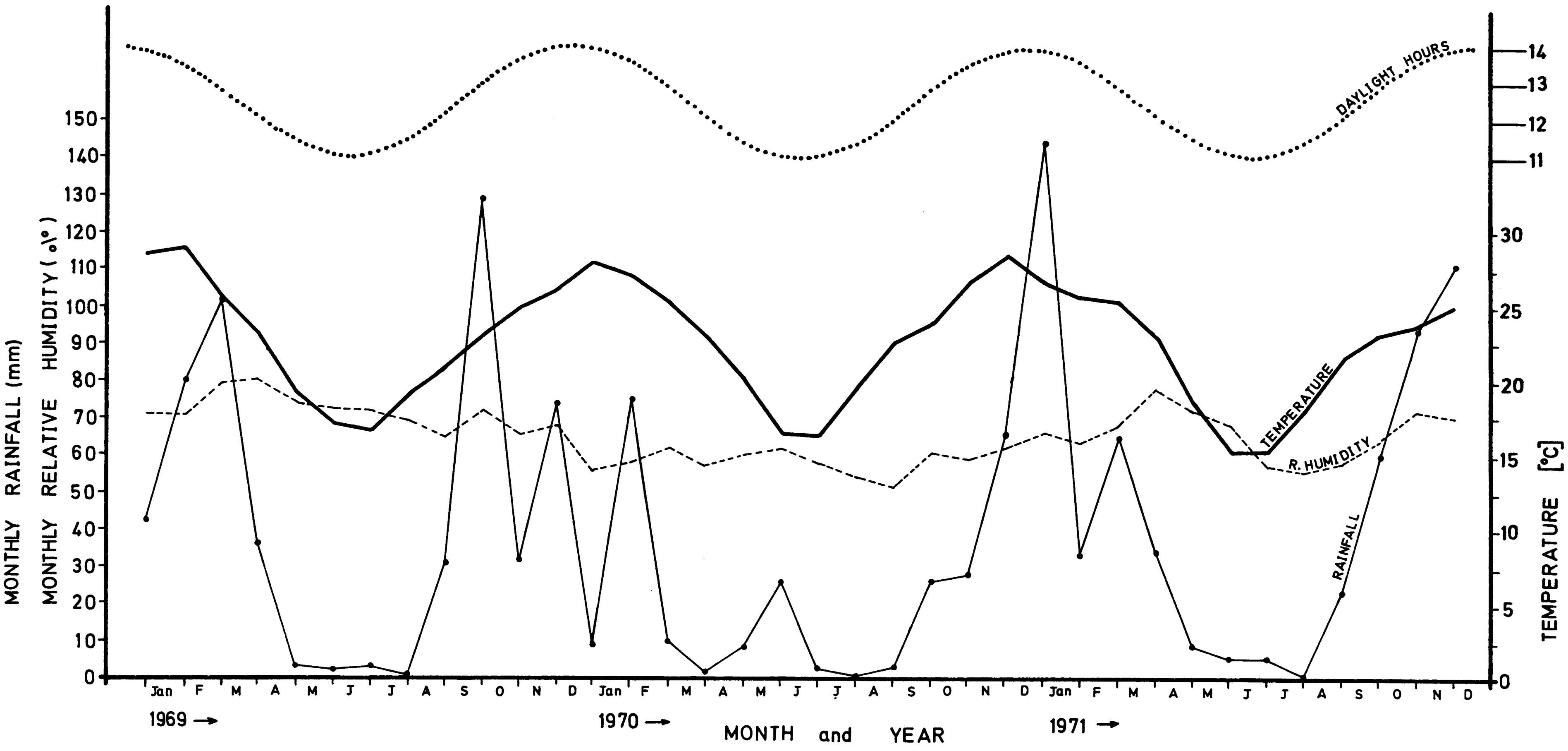


Fig. 1.2. Composite graph of selected climatic variables.

south-east	-	24%	— 75%
south	-	23%	
east	-	15%	
north-east	-	13%	
north	-	10%	
north-east	-	7%	
south-west	-	5%	
west	-	3%	

It is significant that most of the wind blows in from the Mocambique coast - the opposite direction from which most of the rainfall comes.

1.4.2.3. Temperature and Humidity.

In the Kruger Park temperatures may vary between 0°C to over 40°C (Young, 1970).

Abnormally low temperatures of -4,2°C were measured during the winter of 1964 (Van Wyk, 1971). November and December are generally the hottest months, while June and July are the coldest with frost sometimes occurring in low-lying areas on cloudless nights. Mean daily temperatures for Skukuza were calculated by dividing the maximum and minimum daily temperature by two and these were then used to calculate mean monthly temperatures (Fig. 1.2.).

Relative percentage humidity may vary between 100% and less than 10% (Young, 1970). Mean monthly relative percentage humidity was calculated by averaging three daily readings taken at 0800, 1400 and 2000 hours and then calculating the mean for the month. Only readings taken at the Skukuza weather station were used (Fig. 1.2.).

1.4.2.4...../- 9 -

1.4.2.4. Light (radiant-energy).

To determine whether zebra show any seasonal photoperiodic responses with regard to their migratory behaviour, the hours of daylight at latitude 25° south have been plotted (Fig. 1.2.). This data was taken from Sadlier, (1969) and is based on data from the U.S. Naval Observatory. Since hours of daylight are actually required for the central district the readings at latitude 25° south are representative as this area lies between latitude 24° and 25° south.

1.4.2.5. Drought.

Although droughts were experienced during 1969 and especially during 1970 of the study period, the continued effects from earlier drought years will be discussed with reference to present distribution and movement patterns.

1.4.3. Fire.

The use of fire as a management tool has been vehemently condemned yet widely and extensively used all over the world (Harland, 1956). Humphrey (1962) regards it as a natural phenomenon that has been affecting plants and animals on this earth for as long as there has been vegetation to burn. In the Kruger National Park fire is also regarded as an ecological factor and since this vast area is no longer a self-sufficient ecological unit, the whole of the Eastern Transvaal Lowveld being one unit, routine fire management is practised (Brynard, 1964 and Van Wyk, 1971).

To carry out burning programmes effectively the whole of the Park has been divided into some 300 blocks, between 24 and 80 sq. km. in size. These are separated from each other by a network

of fire..../- 10 -

of fire-breaks which are cleared of all vegetation early in the dry season. In contrast to blocks which are burnt either bi- or tri-annually, the following large areas are strictly protected from fire: mountainous regions, important catchment areas, riverine strips or regions around permanent water supplies, swampland or vleis, abused areas where there are signs of erosion or which have suffered severely from drought or overgrazing, unique floristic areas which are preserved as botanical reserves within the Park, regardless of their value as game habitats, and areas with an inherently sparse and vulnerable grass cover, such as on some shallow gravelly soils (Pienaar, 1969c).

The remainder of the Park, except the sour veld regions around Pretoriuskop, is subjected to a system of triannual burning in spring, following the first substantial rains (a precipitation of at least 50 millimetres is essential). The sour veld is burned bi-annually, and here half the area is treated in spring and half in the early autumn.

1.4.4. Biotic factors.

The biotic factors which affect the seasonal and sporadic movements of zebra include animal to plant and animal to animal relationships.

1.4.4.1. Vegetation.

Adequate description of the vegetation and classification of the vegetation types of the study area has been provided by Brynard (1964), Pienaar (1963), Van der Schijff (1957 and 1958) and Van Wyk (1971). In his publication on the "Trees of the Kruger National Park", Van Wyk (1972) gives the most recent and up to date vegetation map of the area. With the author's permission this map has been reproduced and simplified to suit the present publication. (Fig. 1.3.).

1.4.4.2. Large Mammals.

The numerical status of the larger herbivorous species as determined by an aerial and ground census conducted in August 1970 is given in Table 1.2.

Table 1.2.

Numerical status of the larger herbivorous mammals in the Kruger National Park (August, 1970).

Species	Total number in Kruger National Park
Impala	161,950
Buffalo	21,142
Zebra	20,227
Wildebeest	13,950
Elephant	8,821
Kudu	6,520
Giraffe	3,870
Waterbuck	3,307
Warthog	2,917
Sable Antelope	1,033
Nyala	745
Tsessebe	633
Eland	349
Roan Antelope	266

In addition to this, the Park houses a population of some 300 wild dogs (Lycaon pictus); several thousand spotted hyaenas (Crocuta crocuta); less than 200 brown hyaenas (Hyaena brunnea); 300 cheetahs (Acinonyx jubatus); 700-800 leopards (Panthera pardus); and about 1200 lions (Panthera leo).

Chapter 2..../- 12 -

LEGEND

✕ *Diplorrhynchus condylocarpon*/*Burkea africana* woodland with scattered *Androstachys johnsonii* evergreen hardwood forests.

▩ Climax *Colophospermum mopane* forest.

||| *Colophospermum mopane*/*Combretum apiculatum* woodland.

] *Colophospermum mopane* shrub savanna.

▦ *Baphia massaiensis* subsp. *obovata*/*Guibourtia conjugata* scrub with scattered trees (*Xylia torreana*; *Zeroderris stuhlmannii*).

▨ *Colophospermum mopane*/*Combretum apiculatum* woodland of the Lebombo range.

☰ *Combretum apiculatum*/*Acacia nigrescens* woodland.

• *Acacia nigrescens*/*Sclerocarya caffra* woodland savanna.

▧ *Combretum apiculatum*/*Acacia*/*Pterocarpus rotundifolius* woodland of the Lebombo range.

● *Pseudolachnostylis maprouneifolia*/*Strychnos* woodland (Pumbe Sandveld).

■ *Acacia welwitschii* subsp. *delagoensis*/*Albizia evansii* thorn forest.

⁄⁄ *Acacia*/*Combretum* open woodland with closed lower layers.

▩ *Combretum* woodland of the Malelane hills.

∴ *Terminalia sericea*/*Dichrostachys cinerea* subsp. *nyassana* savanna woodland with tall grass.

] *Acacia nigrescens*/*Albizia harveyi* woodland savanna.

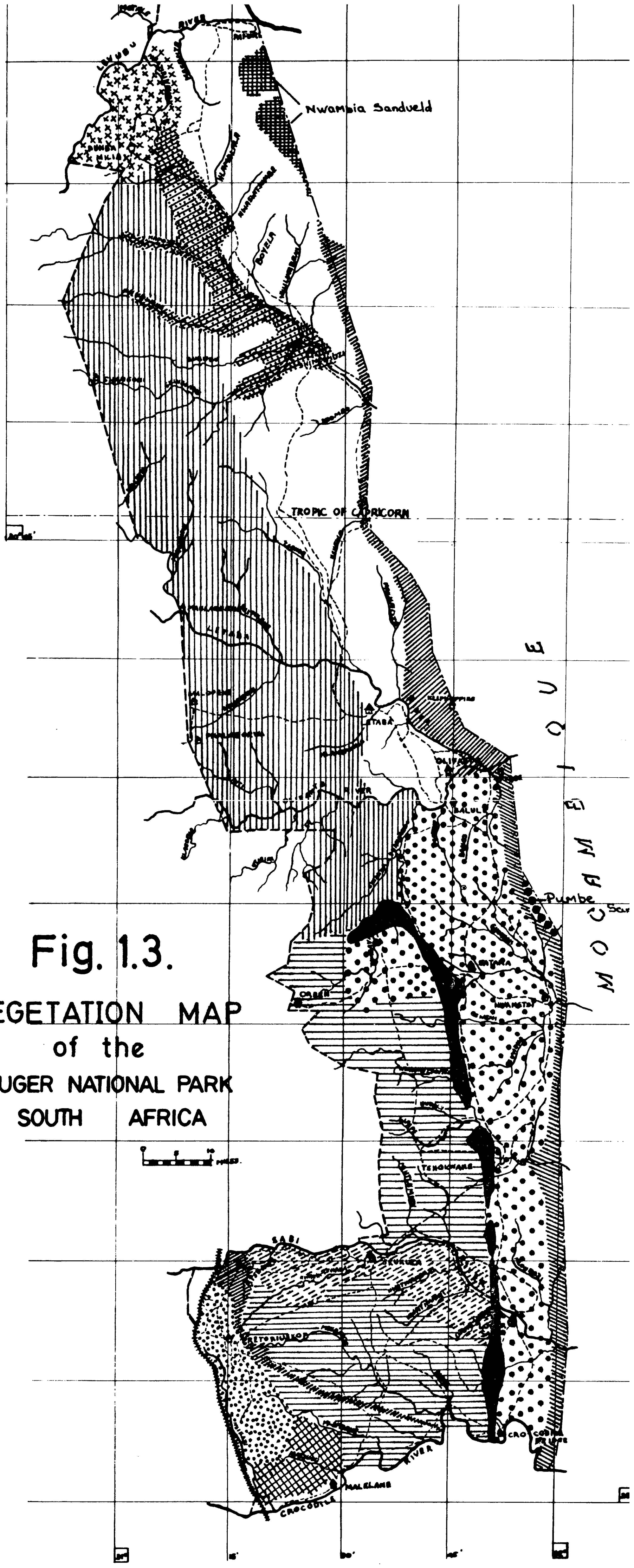


Fig. 1.3.

VEGETATION MAP
of the
KRUGER NATIONAL PARK
SOUTH AFRICA

Chapter 2.

PROBLEM AREAS WITH REGARD TO ZEBRA (AND THEIR HISTORY)

With the appointment of the late Col. James Stevenson-Hamilton as Warden of the Sabi Game Reserve in 1902, the first management policies were initiated. At first these policies were directed at faunal preservation, little attention being given to the flora. However, as the years passed it became increasingly obvious that the herbivorous animals were not only reacting to disease, predation and water shortages, but that the condition of the vegetation was of primary importance. During these years very little was known of the effect of fire on vegetation and in general it was regarded as detrimental. Lack of knowledge on the use and abuse of fire led to varying and often conflicting opinions, with the result that management practices were frequently altered. Prior to 1946, for example, autumn burning was regularly practised by the Warden and his staff (Stevenson-Hamilton, 1930), while after 1946, when Col. J.A.B. Sandenbergh succeeded Stevenson-Hamilton, controlled burning was abolished (Sandenbergh, 1950).

Changes in management practices, some essential and others of doubtful value,together with a number of drought years and a reduced flow in many of the rivers (due to farming and other activities outside the Park) have resulted directly or indirectly in habitat changes which in many cases have proved to be unacceptable to the species here considered.

2.1. Northern..../- 13 -

2.1. Northern district.

Although zebra occupying the vast area north of the Olifants river are by no means overutilizing their habitat, the effect of their competition for water, together with the competition of large herds of elephant and buffalo, is being felt by rarer and more timid game such as roan antelope, sable antelope, tsessebe and waterbuck. In addition to this, the reduced water supplies in the seasonal rivers to the west of the Lebombo flats have resulted in more and more elephant, buffalo and zebra utilizing the artificial waterholes of the Lebombo flats (Pienaar, 1970). These more robust species aggravate the situation by monopolizing and eventually even completely draining a waterhole - to the obvious detriment of the more sedentary species.

At present no zebra are being culled in the northern district, but in the future special checks will have to be kept on their numbers, especially should the eastern boundary be fenced.

2.2. Central district.

In certain regions of the central district overgrazing and trampling by large herds of zebra and wildebeest has become an immediate problem.

The zebra sub-populations referred to in this chapter are discussed in chapter 4 section 4.3., while the exact boundaries between each sub-population are given in Fig. 4.3.

2.2.1. Western boundary sub-population.

Prior to the erection of the western boundary fence these zebra customarily migrated in a general north-south direction. Approximately half of their winter and summer range was, however,

situated..../- 14 -

situated outside the present western boundary of the Park (Pienaar, 1964). With the completion of the fence early in 1961, they were cut off from part of their traditional grazing areas to the west. In addition to this, both zebra and wildebeest used to move in a westerly direction, out of the Park, during the late winter and early spring of dry years. (Stevenson-Hamilton 1947 & 1952; Pienaar, 1970; Van der Schijff 1958 & 1959). These movements were correlated with water shortages in the Park, the game moving westwards towards the better watered foothills of the Drakensberg Mountains. This was, however, a temporary movement and was followed, after the first spring rains, by a north-easterly movement towards the traditional summer (wet season) range.

Before the fence was erected, it was, however, realized that not only would the size of the traditional grazing areas be reduced, but that the game would be cut off from vital watering points, essential during times of drought. In addition, the migratory routes would be cut by the fence in a number of places. To alleviate these problems seven dams were built, mainly in the winter grazing area inside the Park. It was hoped that these would entice the game to utilize areas within the Park, rather than disperse towards the west.

Unfortunately the fence was closed while the migratory herds were still in their summer grazing areas around Kingfisherspruit section and their traditional migration routes southwards, which led across adjoining farms, were obstructed by the fence. When the southward migration commenced the bewildered animals concentrated in masses against the fence, and when the surface waters

dried up..../- 15 -

dried up they were threatened with death (Pienaar, 1970). A crash program to provide water for the stricken game was immediately launched and several successful bore-holes were sunk in the area. Unfortunately the local habitat (summer grazing area) was severely degraded before the zebra and wildebeest could establish new migration routes which circumvented the boundary fence. The problem was further aggravated because some of the game were reluctant to leave the area because of the permanent supply of water.

To alleviate the intense overgrazing and trampling in the region, attempts were made to entice game into the area south-east of Kingfisherspruit by means of spring burns and water provision. These attempts were, however, unsuccessful and it was eventually decided that to save the area it would have to be fenced off. During 1966 this fence, running from the farm Albatros, to just north of Red Gorten windmill (Pienaar, 1965) was erected (see Fig. 4.4.(b)) with the hope that it would deflect the game eastwards towards potentially good, yet unfamiliar, grazing areas.

The recovery of the degraded area has subsequently justified the erection of this fence to the extent that it could be removed during January 1972.

In addition to the eastward extension of the traditional summer grazing area, the zebra and wildebeest have been able to shift the boundaries of their winter grazing area both in a southerly and an easterly direction, the result of this being that during dry years they once more drink from the Sand river and even from the Sabi, east of its confluence with the Sand.

Since 1969 there have unfortunately been indications that

the numbers..../- 16 -

the numbers of zebra utilizing the western boundary area (Fig. 4.3. Unit (5)) are decreasing. This is possibly due to the fact that a large portion of their traditional summer grazing area on the dolorite reef has progressively been excised by the two previously mentioned fences. The zebra and wildebeest that left this area are believed to have joined up with the Satara and eastern boundary sub-populations.

The recent removal of the fence between the farm Albatros and Red Gorten windmill, may eventually lead to a return to the normal population level within this area.

2.2.2. Eastern boundary sub-population.

With respect to this very successful sub-population, the following reasons may be regarded as being contributory to the degraded state of portions of their summer grazing area: the misplacement of Mazithi dam and windmill; gravel pits excavated by road building teams on the Lindanda plains. These pits often retain their water during the dry season; their numerical increase during the past seven years; a number of very dry years between 1960 and 1970; their stubborn insistence to return to traditional summer grazing areas.

As is the case with the western boundary sub-population, these zebra practice a natural system of rotational grazing, whereby each seasonal grazing area has a portion of the year in which to rest and recover from the previous season's intense grazing. Unfortunately only winter grazing areas are afforded complete rest during the growing season, the summer grazing areas often being utilized as soon as the first grasses start sprouting. Due to this, the summer grazing areas of migratory game are more suscep-

tible to..../- 17 -

tible to trampling and overgrazing, even though their area is larger than winter ranges.

When artificial watering points were provided after 1945, knowledge of the grazing behaviour and movement of game was lacking, and consequently artificial watering points were frequently put down in areas which were chosen almost entirely on subjective criteria (Pienaar, 1970). In this manner a number of watering points were established in traditional summer grazing areas, where they did more harm than good. One such misplaced watering point, with regard to the eastern boundary zebra, is Mazithi dam and windmill (Pienaar, 1970; Van der Schijff, 1959). This watering point lies in the transitional zone between winter and summer grazing areas and is unfortunately close enough to the Lindanda summer range to serve game there with water towards the end of the wet season. Its effect is thus to keep game (zebra and wildebeest) on the plains after the seasonal veld pans have dried up. Together with the factors previously mentioned, the final result has been the overutilization of the Lindanda area.

The natural course of events in an overutilized wet season range would be a reduction in available surface water and a consequent shorter period of utilization by the migrant game. The region would thus have a longer time in which to recover.

2.2.3. Satara sub-population.

In contrast to the two previously mentioned sub-populations, the Satara zebra are sedentary and consequently quite a different set of conditions control and influence their seasonal movements.

Certain portions of their habitat, especially the basaltic soils north of Gudzani windmill (Fig. 2.1.), are prone to overgrazing. This area, and especially the region around Bangu windmill, has retrogressed alarmingly in recent years. The retrogression has in most cases been typified by an infestation of the unpalatable "stinkgrass" Bothriochloa insculpta (Fig. 2.2.). This grass is poorly utilized by most grazing species except zebra and wildebeest and is particularly favoured in its competitive association with other more palatable species - a situation which lends itself to selective grazing and deterioration of the habitat (Pienaar, 1963; Van Wyk, 1965). The poor condition of the habitat may additionally be ascribed to the uncanny way in which summer rains have tended to miss the Bangu area, together with the always available strong supply of underground water at this windmill, to the lack of supporting waterholes in the vicinity to reduce the grazing pressure around Bangu, and to the shallow soils of the area.

2.3. Southern district.

In the southern district the zebra population poses two problems:

(i) rapid increase in numbers in certain areas (Crocodile Bridge sub-population),

(ii) slow increase in numbers in potentially good areas (Pretoriuskop zebra).

2.3.1. Crocodile Bridge sub-population.

Although this area (Fig. 4.3., Unit (8)) is not showing any signs of serious overgrazing the habitat is being heavily utilized by large herds of buffalo and zebra. During recent years the growth

curve of..../- 19 -

Fig. 2.1. Heavily utilized zebra and wildebeest habitat north of Gudzani windmill, May, 1971.

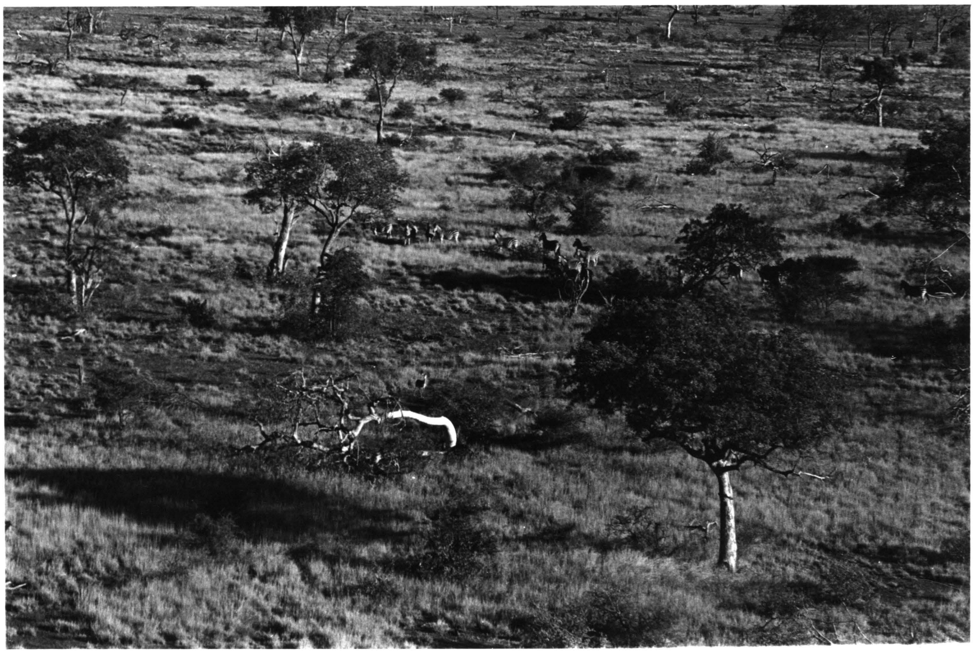


Fig. 2.2. *Bothriochloa insculpta* infestation due to the selective grazing habits of zebra and wildebeest. Near Marheya windmill, May, 1971.

curve of this zebra sub-population has shown a marked upward trend and this is believed to be due to:

(i) the misplacement of Mhlanganzwane and Mpanamana dams (Pienaar, 1965). These two dams were built in the heart of the summer grazing area with the result that both zebra and buffalo utilize the area almost throughout the year. The mosaic of waterholes formed by these two, together with Gomondwane windmill, Mkohlolo dam, the Sabi and the Crocodile rivers, has resulted in an ideal situation for the herbivorous species. The reduced distances between waterholes, together with the unfavourable situation created with respect to the larger predators has reduced mortality rates and promoted population growth,

(ii) zebra form a minor part of the lion's prey in this section. Analysis of the carcasses of game animals killed by lions show that 36,15% of their kills consist of impala; 26,41% of buffalo; 11.15% of waterbuck and only 9,27% of zebra (Pienaar, 1969b). It is obvious therefore that these species form effective buffers with respect to zebra depredation.

From the above it is clear that the misplacement of artificial waterholes has initiated a population explosion favourable to certain herbivorous species and in particular the zebra. This increase has in turn resulted in localized grazing problems due to changes in the natural rotational grazing system.

2.3.2. Pretoriuskop zebra.

When comparing the distribution of zebra in the southern district (Fig. 4.1.) with their relative abundance in the same area (Fig. 4.2.), one can clearly see that large areas are very sparsely populated. These patterns reflect the reaction of the species to the habitat, and will be discussed in chapter 4. It is, however, commonly known that Pretoriuskop section used to carry a large population of both zebra and wildebeest. The factors contributing to the present reduced population level will now be discussed in some detail.

In the years prior to the second world war the habitat of the Pretoriuskop area consisted of a shorter grassveld and relatively little bush, with significant herds of game such as zebra, wildebeest, sable antelope and waterbuck.

Prior to the proclamation of the Park in 1926, trek farmers used to enter the area annually during the winter months, with their stock. However, to ensure that fresh grazing would be available during these months, they customarily burnt the range during autumn (February or March). The result of this practice was the selective utilization of large burnt areas by domestic stock during the winter, game continuing the process during the ensuing summer months (Van Wyk, 1965). Selective utilization of the grasses particularly favoured the tall unpalatable thatch grass Hyperthelia dissoluta which is very poorly utilized when mature. Over the years this grass increased very slowly and it was only after 1947 when all burning in the area was terminated that the species started to encroach rather dangerously. Concomitant to the encroachment of Hyperthelia was the tremendous increase in fire resistant shrubs which were previously burnt back by the annual fires.

For seven years (up to 1954) the area was left almost entirely unburnt, the eventual result being a change to a predominantly long grass veld with thick bush. This change was largely unacceptable

to the..../- 21 -

to the previously mentioned species, and they subsequently gradually emigrated from the area to surrounding Bantu Trust areas where annual burning was still practised. In contrast to this, browsing species such as kudu and impala showed a marked upward trend in their growth curve, while reedbuck were also afforded ample habitat in the grassy vlei areas.

During 1957 (Brynard, 1964) a biannual rotational burning scheme of alternate autumn and spring burning was initiated. The result of this program has since been a slow but noticeable recolonization of the region by species which formerly inhabited it.

Chapter 3..../- 22 -

Chapter 3.

MATERIALS AND METHODS

3.1. General

Work was conducted throughout the Park and at all times of the year and for this reason a suitable vehicle was essential. A four wheel drive Land Rover was found to meet these requirements. Photographic equipment included a Minolta SR_7 camera with a range of interchangeable lenses from 55 mm to 400 mm. Depending on the nature of the work, either 8 x 30 or 10 x 50 binoculars were used.

Except for certain remote areas in the northern part of the Park, zebra could be effectively approached by vehicle and the necessary observations carried out. Flight distances varied from between 40 and 80 metres, although in areas only occasionally visited by staff, zebra ran off at the sight of a vehicle. This factor was later to hamper the marking program in certain localities.

In addition to observations made from the ground, aerial reconnaissance was extremely valuable. The Bell helicopter regularly used in the Park for census, culling and game capture programs proved to be invaluable, especially with respect to the plotting of seasonal distribution and migratory patterns. Only when systematically flying over an area as vast as the Kruger Park does one gain an all-encompassing picture of the habitat, topography and some of the other factors likely to influence game distribution and movement. It was unfortunately not possible to fly the entire study area, but fairly intensive flights were made in the central district and parts of the northern

district..../- 23 -

district. During these flights a total of some 45 flying hours was registered.

Local movements, migratory patterns, seasonal distribution and home ranges of zebra throughout the Park were initially plotted on suitable large scale maps (1:100 000 or 1:125 000) and subsequently transcribed onto smaller maps suitable for this publication.

Observations made in the field on the eruption and replacement of deciduous incisors and the eruption of permanent incisors were augmented by data collected from animals kept in captivity at Skukuza. (Fig. 3.1.) These captive zebra also served to elucidate certain behavioural aspects less easily obtainable under field conditions. Zebra captured and retained in captivity for varying periods of time are given in Table 3.1.

Table 3.1.

Zebra kept in captivity at Skukuza during the study period

No.	Date of capture	Age of first observation	Sex	Period in captivity	Remarks
1	2.6.69	1 year	♀	1 year	Killed by lion
2	2.6.69	5-6 years	♂	2 years 10 month	-
3	11.8.69	7-9 years	♀	2 years 4 months	-
4	9.2.70	± 3 days	♂	1½ months	-
5	9.1.70	± 5 days	♀	1½ months	-
6	14.3.70	Birth	♂	1 year 10 months	Born in captivity
7	4.5.70	± 3 weeks	♀	6 months	Sold
8	7.7.70	12 days	♂	6 months	Sold
9	23.10.70	5-6 years	♀	1 year 3 months	-
10	12.1.72	Birth	♀	-	Born in captivity
11	31.1.72	Birth	♀	-	Born in captivity

These..../- 24 -

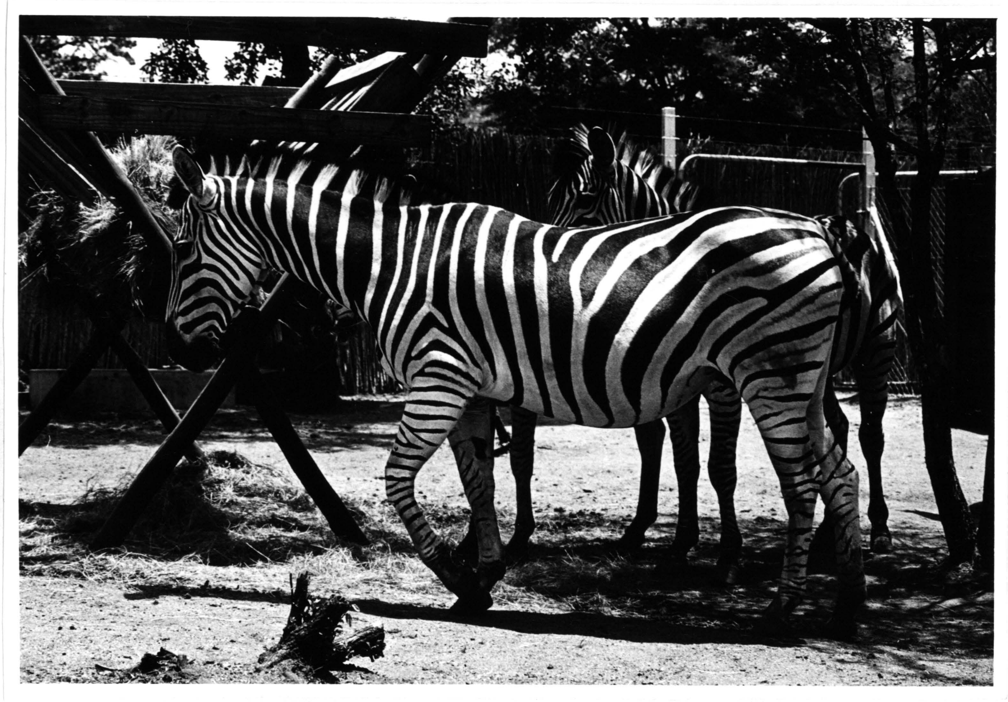


Fig. 3.1. Captive zebra in the study bomas at Skukuza.

These animals were kept in bomas measuring 60 x 30 metres and fed commercially available lucern and **teff grass,** as well as grass specially harvested in the veld. Young foals were bottle fed 3 times per day on a mixture of: full cream powdered milk,
saturated slaked lime water,
2-3 fowl eggs,
crushed thalazole pellets ($\frac{1}{2}$ pellet per feeding session). Feeding continued throughout the period in captivity, although the volume was reduced as water drinking and grass feeding increased.

3.2. Capture and Marking Program.

3.2.1. Purpose and justification for the marking program.

Since the seasonal movements and migrations undertaken by zebra have a bearing on the well-being of this species as well as many other associated ones, it was decided that the marking of a number of individuals in as large an area as possible should be undertaken.

Subsequent to the erection of the western boundary fence, which spans the entire length of the Kruger Park, various changes have taken place in the traditional migratory patterns of zebra and wildebeest in the central district. These changes have resulted in serious localized habitat degradation and the necessary instigation of various remedial management practices. These, especially with respect to the Kingfisherspruit section, are discussed in a later section.

With the proposed erection of a game-proof fence along the eastern boundary of the Kruger National Park, a knowledge of game

movements..../- 25 -

movements throughout the Park is also essential - especially with regard to the future water purveyance program. In addition to these considerations, marked zebra would provide data on various aspects of their social behaviour and could be used to derive a series of age classes for the sub-adult and adult segment of the population.

3.2.2. Number of Zebra marked and their respective localities.

During the years 1969 and 1970 a total of 89 zebra of both sexes, and ages ranging from one year to old age were marked in the Kruger Park. Since the central district is a problem area with regard to zebra and, additionally, houses just over 60% of the total population, most animals were marked here. Distribution of the marked zebra between the three districts was as follows:

Northern district - 13
Central district - 59
Southern district - 17

The selection of marking localities depended on the zebra concentration in the area and its importance as a zebra habitat. In no case were more than two zebra marked in the vicinity of the same waterhole, the result being a dispersion of marked specimens over the study area. Due to a shortage of time and money and the extreme wariness of certain zebra herds in the northern district, it was only possible to mark animals as far north as Nshawo No. 5 windmill. Movements plotted for zebra north of the Tihongonyene windmill were based on observations made on distribution patterns at different times of the year, augmented by the daily observations of the local Rangers and Biologists. An understanding of the game movements in the area between the Letaba and Shingwidzi rivers later also helped to elucidate the more northerly movements, where a similar

pattern..../- 26 -

pattern exists. In addition to this, data collected from 52 zebra marked in the central district between 1963 and 1965, by the biological staff, were placed at my disposal. In this project zebra were marked in six different areas at different times of the year. The marking areas, subsequently referred to as marking stations, were located as follows:-

i) Lindanda - 26 marked,
ii) Between Sweni windmill and Milaleni windmill - 6 marked,
iii) South of Mnondozi dam - 7 marked,
iv) Nwatindlophu river mouth - 7 marked,
v) Nwatindlophu windmill - 6 marked.

The movements discussed in this paper thus relate to the behaviour of 141 zebra, individually marked and followed-up over the periods 1963 to 1966 and 1969 to 1971.

3.2.3. Immobilization procedure and drugs used.

Because of the high cost of immobilizing and tranquilizing drugs a number of different drugging procedures were applied. In all cases animals were darted from the inside of a vehicle using dart syringes propelled by the Van Rooyen crossbow. For a description of this equipment the reader is referred to Van Niekerk and Pienaar (1962); Pienaar, Van Niekerk, Young, Van Wyk and Fairall, (1966a) and Pienaar et. al. (1966b).

Drugs used in the study included the following:

(i) Narcotics and analgesics

(a) Etorphine hydrochloride or M.99 (Reckitt). This thebaine derivative chemically related to morphine was administered at the rate of 3 mg per adult animal.

Zebra..../- 27 -

Zebra in the Kruger Park appear to have a greater resistance to this drug than in East Africa where they are captured with similar mixtures containing only 1,25 to 1,6 mg of M.99. (Klingel, 1968c).

(b) Acetyl-propylorvinol hydrochloride or M.183 (Reckitt). This is essentially the acetylated form of M.99 and the two were used interchangeably. Dosage rates for M.183 were between 3 and 4 mg per adult animal.

(ii) Tranquilizers.

(a) Azaperone (R1929) (Janssen). On hot days Azaperone was used in preference to Acetylpromazine and at a standard dosage rate of 200 mg per animal. This dosage rate was derived from similar ones used by Pienaar (1968a, 1969a).

(b) Acetylpromazine (Boots). The standard dosage rate of 20 mg per animal using this neuroleptic appears to be rather low compared to the 28-36 mg used by Klingel (1968c), and may, to a certain extent, account for the higher dosage of M.99 required.

(iii) Parasympatholytic.

(a) Scopolomine (Hyoscine hydrobromide). According to Harthoorn (1965) this drug causes dilation of the pupil and paralysis of accommodation by affecting the impulses to the iris and ciliary muscles of the lens. Due to photophobia and the animal's incapability of focusing on nearby objects, it is thus more easily captured. Although a helpful adjuvant to drug mixtures employed for the

capture..../- 28 -

capture of zebra (Pienaar et. al. 1966a), it may, due to its long-lasting effect, handicap a marked animal's chance of survival. For this reason scopolomine was only used when capturing zebra in more open areas. In dense vegetation they were inclined to stumble about blindly, frequently injuring themselves. Scopolamine was administered at a rate of 10 mg per zebra.

The above-mentioned drugs were used in the following combinations:

M.99 or M.183 plus either Azaperone or Acetylpromazine.

In all cases the addition of Hyoscine hydrobromide was optional.

(iv) Morphine antagonist.

(a) Nalorphine hydrobromide (Burrough's-Wellcome). This antidote was used to antagonise the effect of both M.99 and M.183, and was administered intravenously at a rate of 100 mg/zebra.

(b) M.285 (Reckitt). This potent Etorphine specific antagonist was occasionally used, and at a rate of 5 mg per zebra when Nalorphine hydrobromide was in short supply.

(v) Muscle relaxants.

(a) Succinylcholine chloride. In contrast to the narcotic M-drugs previously mentioned, Succinylcholine chloride or Scoline is a potent muscle relaxant. Although extremely cheap, the disadvantages of its application as a routine field immobilization agent tend to outweigh the advantages.

Since..../- 29 -

Since animals are extremely sensitive to an overdose of the drug, one has to estimate their weight before preparing the appropriate dart syringe. To save time, seven or eight darts were filled with dosages of the drug that covered the range of body weights for the capture of adult stallions. It was found to be unpractical to use Scoline on mares since it was too difficult to estimate their weights. With a dosage rate of 0,1 mg per lb., darts containing between 70 and 85 mg were prepared and stored on ice in a cool-box. Once the specimen for marking had been chosen, the appropriate dart could be selected. The advantages of this drug include:

(a) It is very cheap.

(b) No antidote or neuroleptic required.

(c) Provided the animal's weight is correctly estimated and none of the drug leaks out through the dart wound, the zebra is fully recumbent within three to four minutes.

(d) On recovery the animal is almost 100% normal.

Disadvantages:

(a) More time is required to prepare the dart syringes.

(b) The drug is sensitive to heat when in the dissolved state.

(c) The darted animal's weight required accurate estimation. In this respect an overdose results in death due to anoxia, while an underdose has no effect on the animal. Expensive dart syringes are thus frequently lost.

(d) The..../- 30 -

(d) The recovery time is between six and 20 minutes and is frequently not long enough for marking procedures.

(e) It is almost impossible to work on the teeth of a Scoline drugged zebra due to the animal's vicious biting and kicking reactions.

Although a number of zebra were successfully captured with this drug occasional deaths were inevitable and hence the oral administration of medical oxygen was attempted. Using a standard endotracheal tube and a portable oxygen cylinder, overdosed zebra were intubated and the lungs ventilated with the oxygen. This technique, however, proved to be too time-consuming, while the apparatus was also rather delicate and bulky. In addition a gag through which the endotracheal tube could be passed had to be forced into the animal's mouth, otherwise the zebra would damage the tube with its vicious biting. Difficulty was also experienced in finding the glottis, the tube being more inclined to slip down the oesophagus. As a final test the tranquilizing drug, Rompun-HCl (Bayer), also designated Bay Va 1470, was tried in combination with Scoline. Results obtained from three adult stallions immobilized with the normal Scoline dose plus 1½ ml of the 10% solution of Rompun, gave the following reaction times:

(a) Animals recumbent - 2½, 1¾ and 3 minutes after darting.

(b) Animals fully ambulant - 10, 4 and 7 minutes respectively after darting.

Although these were fantastic reactions to witness, they did not leave enough time for the marking procedure. For obvious reasons these experiments were abandoned and only the M-series

of drugs..../- 31 -

of drugs were used.

As soon as the marking procedure had been completed all dart wounds were treated with a solution of Terramycin (Pfizer) and should the animal have sustained any additional injuries a precautionary intramuscular injection of $6\frac{1}{4} \times 10^6$ units of the penicillin compound, Triplopen (Glaxo-Allenbury's) was administered.

3.2.4. Marking techniques.

Certain factors had to be considered before deciding on a specific marking technique. These include:

(i) The success or failure of the study depended on the collection of sufficient and simultaneously reliable resightings. These factors in turn depend on how clearly the animal is marked and its chances of being spotted amongst a large herd where dense vegetation could obstruct one's vision. Since both tourists and staff were asked to report on the localities of marked individuals, it was essential to devise a method that would take up as little of their time as possible and also be foolproof.

(ii) The marking technique had to be of such a nature that the marked specimen could be recognised for a period of at least one year. This was important because certain of the marked individuals had to have their incisors measured after this interval.

(iii) Each zebra had to be marked individually, i.e. no two animals could bear the same mark.

Taking..../- 32 -

Taking cognisance of these factors, it was decided that a suitable and easily recognisable collar (Fig. 3.2.) was essential and that devices such as ear tags, cropped tails and rump brands would be used to increase the chances of spotting the marked animal. Should a collar be lost, numbers branded on the rump would be essential for the re-identification of the specimen.

Although both stallions and mares were initially marked with collars, it was later discovered that a number of stallions had either lost their collars or were in the process of losing them. For this reason more mares were marked than stallions, the mares showing no inclination to rid themselves of the collar. When observing the vicious fights between adult stallions one can clearly see that the neck region is the spot to which most biting is directed. Fighting, especially during the mating season, together with the animal's habit of rubbing its neck against objects results in tearing and eventual loss of the collar. In the case of mares no collars were lost and tearing was never observed.

3.2.4.1. Collars used.

"Sterkolite" (Kahn and Kahn), a commercially available polyvinyl plastic material impregnated with nylon thread, was utilized. This tough material has been used for marking various game species throughout South Africa and South West Africa. In the Kruger Park it has also been used to manufacture collars for cheetah, lion and tsessebe (*Damaliscus lunatus lunatus*). The durability of the material, the bright colours and the ease with which it can be cut ensure its practical application.

Field..../- 33 -

Fig. 3.2. An adult stallion with a white "sterkolite" collar, cropped tail and number 2 branded on his rump. These collars remained serviceable for two years.

Field tests with the various colours available indicated that red and white were most easily spotted, blue being less contrasting when used on a zebra. The method employed was to use two strips of differently coloured heavy duty "Sterkolite", numbers or letters being cut out of the top strip, and then the two strips were glued together. The dimensions of the collar and the spacing of the numbers or letters are given in Fig 3.3. To further reinforce the collars and prevent bending and rolling of the material, four strips of celluloid measuring 2" x 4" x $\frac{1}{10}$" were spaced between the four numbers cut out of the upper layer of "Sterkolite". After glueing the two layers together with "Bostik 1769" (Kahn & Kahn), brass split rivets and nylon thread were used to support the two layers and keep the celluloid strips in position. Three steel bolts ($\frac{1}{2}$" x $\frac{1}{4}$") and nuts together with galvanised body washers (diameter $1\frac{1}{2}$") were used to fix the collar round each animal's neck. (Fig. 3.4.).

Because certain numbers or letters could create confusion, only the following were used:

Numbers:- 1, 2, 3, 4, 5, 7, 8, 11, 12, 13, 14, 15, 17.

Letters:- E, F, G, H, J, K, N, S, T, U, V, X, Y.

Squares and circles were also used as patterns, in place of numbers or letters.

Before the collar was fastened the centre of the mane was cropped to a width of about 20 cm and the tail either completely stripped of its hair or cropped level with the last caudal vertebra (Fig. 3.2.). Coloured eartags were occasionally fitted, although they were quite worthless as far as resightings were concerned.

Rump..../- 34 -

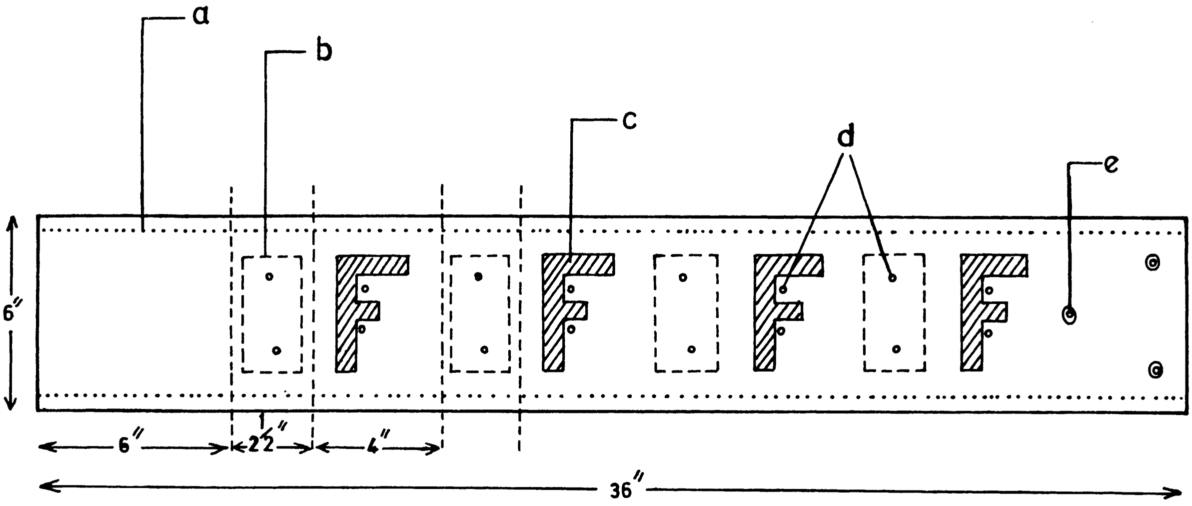


Fig. 3.3. Plan and dimensions of collars used.
(a) Stitching along edge (nylon thread).
(b) Position of celluloid strips between "sterkolite" layers.
(c) Letter cut out of upper section of "sterkolite".
(d) Supporting rivets.
(e) Bolts and washers for fastening collar.

Fig. 3.4. Fastening a blue "sterkolite" collar. Note the nylon stitching, the large washers and the supporting rivets.

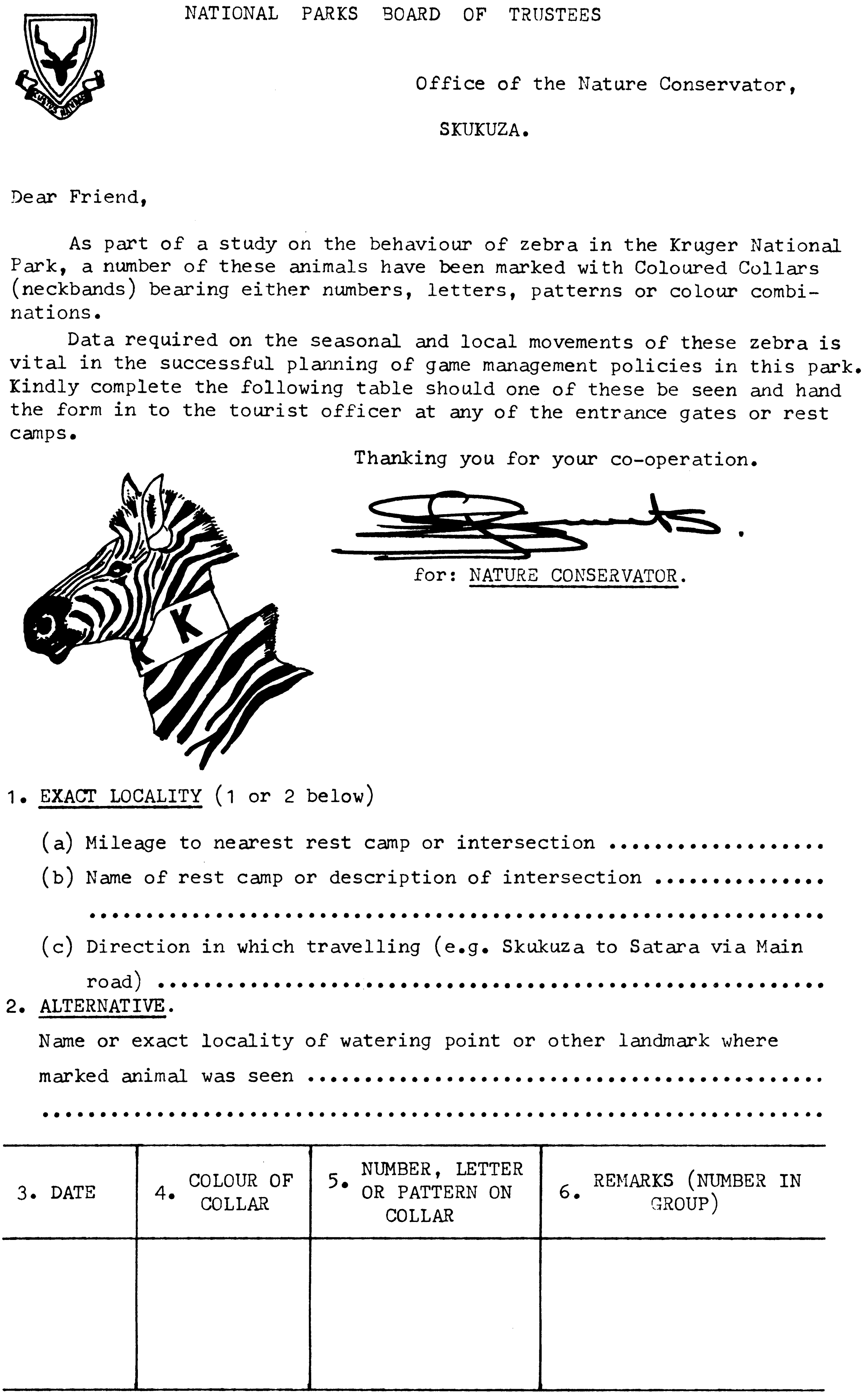
Rump branding (Fig. 3.2.) although of some value, later proved to be unnecessary as all collars lasted well (Fig. 3.5.). In the open savanna plains of East Africa where hundreds of zebra could be observed at a time, Klingel found that collars were unnecessary. In his study most animals were branded, ear-tagged and the mane and tail trimmed (Klingel 1967, King and Klingel 1969).

3.2.5. Collection of data on Marked Zebra.

To stimulate an interest in marked zebra and hence promote the collection of resightings, photographs with suitable captions consisting of a short description on the objectives of the study, were displayed in all the tourist camps and at the entrances to the Park. Special forms were also printed and made available to both tourists and staff (Fig. 3.6.). After a marked animal had been spotted the appropriate form was completed and later returned to Skukuza. This method proved to be extremely successful and a total of some 1200 resightings were collected in this way.

Chapter 4..../- 35 -

Fig. 3.5. Marked group (1 adult ♂+ 2 adult ♀♀). At this stage the white collar with a blue letter "S" was 1½ years old. The "2" of the number "26" branded on both sides of the rump is just visible on the mare's right rump.



NATIONAL PARKS BOARD OF TRUSTEES

Office of the Nature Conservator,

SKUKUZA.

Dear Friend,

As part of a study on the behaviour of zebra in the Kruger National Park, a number of these animals have been marked with Coloured Collars (neckbands) bearing either numbers, letters, patterns or colour combinations.

Data required on the seasonal and local movements of these zebra is vital in the successful planning of game management policies in this park. Kindly complete the following table should one of these be seen and hand the form in to the tourist officer at any of the entrance gates or rest camps.

Thanking you for your co-operation.

for: NATURE CONSERVATOR.

1. EXACT LOCALITY (1 or 2 below)

(a) Mileage to nearest rest camp or intersection ....

(b) Name of rest camp or description of intersection ....

....

(c) Direction in which travelling (e.g. Skukuza to Satara via Main road) ....

2. ALTERNATIVE.

Name or exact locality of watering point or other landmark where marked animal was seen ....

....

3. DATE	4. COLOUR OF COLLAR	5. NUMBER, LETTER OR PATTERN ON COLLAR	6. REMARKS (NUMBER IN GROUP)

Fig. 3.6. Printed form used for the collection of data on marked zebra. Over 10 000 of these forms were distributed to tourists and staff.

Chapter 4.

THE DISTRIBUTION, MOVEMENTS AND MIGRATION OF ZEBRA.

Although zebra are largely confined within the boundaries of the Kruger National Park, significant local movements and full scale migrations still take place. Certain movements even take zebra outside the present boundaries of the Park.

All movements and migrations are of vital importance to the well being of the population and additionally have a profound indirect effect on the vegetation.

4.1. Present distribution and population density.

The distribution of large mammals in the Kruger National Park has been described by Pienaar (1963). Since this time, however, changes have taken place especially with regard to density and seasonal distribution. These changes are largely due to the provision of new watering points.

The winter distribution and density of zebra derived by an extensive aerial and ground census conducted during August 1971 can be gauged from Fig. 4.1. The true winter and summer grazing areas are illustrated in Fig. 4.4. (a), (b) and (c). To give an idea of the actual numbers of zebra in the different Ranger sections of the Park, Fig. 4.2. has been included. This shows the administrative division of the Park into 14 Ranger sections, with the actual number of zebra counted in each section. From this map and the previous one, one can clearly see that the greatest numbers are found towards the east of

the Park..../- 36 -

the Park and in the central district. The numerical distribution among the three districts is provided in Table 4.1. (1970 census).

Table 4.1.

Numerical status and density of zebra in each of the three districts of the Kruger National Park (August, 1970)

District	Number of Zebra	% of total population	Size of district (Hectares)	% of total area	No. of hectare per zebra
North	5 382	26	997181	52	185
Central	12 285	61	551687	29	45
South	2 560	13	352251	19	138
	20 227	100	1901119	100	

Average number of hectare per zebra for the whole Kruger Park = 94 (2.76 zebra per sq. mile).

From this analysis it is clear that the central district carries three and four times the number of zebra per unit area than do the southern and northern districts respectively.

4.2. Division of the population into sub-populations.

According to Owen (1966) migration is defined as "a regular movement to and from a breeding area", the shift of the population from one place to another being for the purpose of breeding. Lack (1954) proposes a similar definition, but also mentions three other types of movement with which migration intergrates:

(i) movements correlated with seasonal changes in the habitat,

(ii) movements..../- 37 -

(ii) movements made in direct response to harsh weather,

(iii) emigration.

Migration is distinguished from (i) by the greater length of the journey and by the fact that the winter quarters lie in a fixed direction from the breeding area instead of in various directions from it. The movements classified under (ii) are irregular, can occur at any time of the year and do not occur every year. Emigration is also irregular and is a one way movement (Smith, 1966).

Although there are many definitions for the word "migration" (Barnard, 1961) the basic definition appears to require a two-way movement, involving a return to the area originally vacated. The fact that many definitions include that the movement be to and from a breeding area, probably stems from the typical bird migrations between polar and temperate zones.

On the basis of behavioural characteristics and considering the above-mentioned possibilities the zebra population of the Kruger Park may be divided into:

(a) migratory sub-populations,

(b) semi-migratory sub-populations,

(c) sedentary sub-populations.

The word sub-population is merely used to indicate the individual qualities of one portion of the Park's population as compared to another, and by no means infers geographical isolation.

According to Eloff (1959) "an animal that lives a wandering life is called a nomad, but whereas some animals wander more or less

sporadically..../- 38 -

sporadically within a certain geographic region during most of the year, others may have restricted quarters for part of the year, usually in winter, roaming about over a wider area for the rest of the year". In this respect the semi-migratory and sedentary sub-populations could also be called nomadic. The movements of the sedentary sub-populations are, however, confined to a relatively small area (home range) while those of the semi-migratory sub-populations are directional.

By further analysing the movements of zebra, it becomes clear that in conjunction with their sedentary or migratory characteristics, each sub-population tends to utilize a specific portion of the Park i.e. the Kruger National Park can be divided into eight units (Fig. 4.3.), each unit being an ecologically self-sufficient entity with respect to zebra habitation.

The reasons for dividing the Park into these units include:

(i) each unit or sub-population is a fairly distinct entity, its members seldom mixing with those of other sub-populations. When mixing occurs, it is usually of a temporary nature and undertaken by only a few individuals,

(ii) sub-populations are frequently separated by well defined temporary barriers. These barriers are by no means impassible, but act as effective filters between sub-populations, at times allowing little or no mixing. These barriers are either in the form of perennial or annual rivers, thick zebra deterrent bush, very hilly or rocky, or other marginal habitats. In this context the word "barrier" is not used in a strictly zoogeographic sense (see Darlington, 1957),

(iii) for..../- 39 -

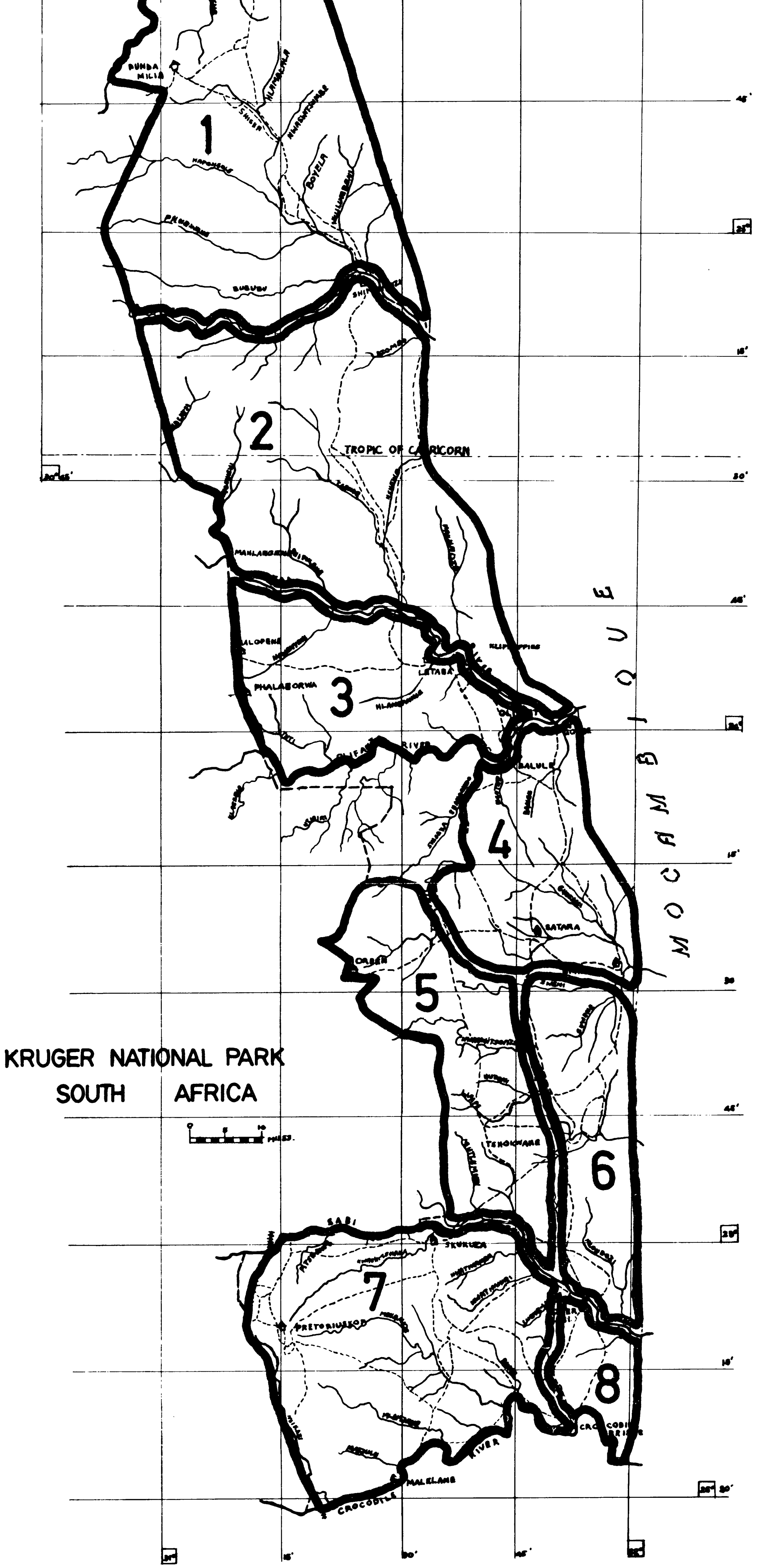


Fig. 4.3. Eight ecologically self-sufficient zebra sub-populations (Units 1 to 8).

(iii) for management purposes it is essential to sub-divide the population, since control programs are only carried out in certain units.

4.3. Discussion of the boundaries of each sub-population and the movements undertaken by the zebra of each unit.

The sub-populations to be defined were separated on the basis of information collected from the following sources:

(i) the local movements and/or migratory habits of 141 zebra marked between 1964 and 1970,

(ii) observations on the seasonal distribution of zebra herds both from the air and from the ground. These observations not only gave the distribution patterns, but also the numbers in each specific unit. Through the use of these figures a check could be kept on the population level for each unit - a marked change between adjacent units would obviously mean that mixing had occurred,

(iii) certain boundaries between sub-populations are seldom crossed, and when this occurs, few animals undertake the crossing, the whole incident being regarded as rather unusual.

4.3.1. Migratory sub-populations.

The true migratory zebra can be separated into two sub-populations:

(a) western boundary zebra (Fig. 4.3. Unit (5)),

(b) eastern boundary zebra (Fig. 4.3. Unit (6)).

4.3.1.1. Discussion of the boundaries and barriers between these two sub-populations and others.

Although the factors contribution to the separation of

these two..../- 40 -

these two sub-populations from one another are not very rigid, they are effective enough to warrant separation for management and descriptive purposes.

Mixing does occur between the two, but is usually on a very small scale. The routes along which mixing occurs between these sub-populations and between the Satara zebra are indicated by the bruken lines in Fig. 4.4.(b).

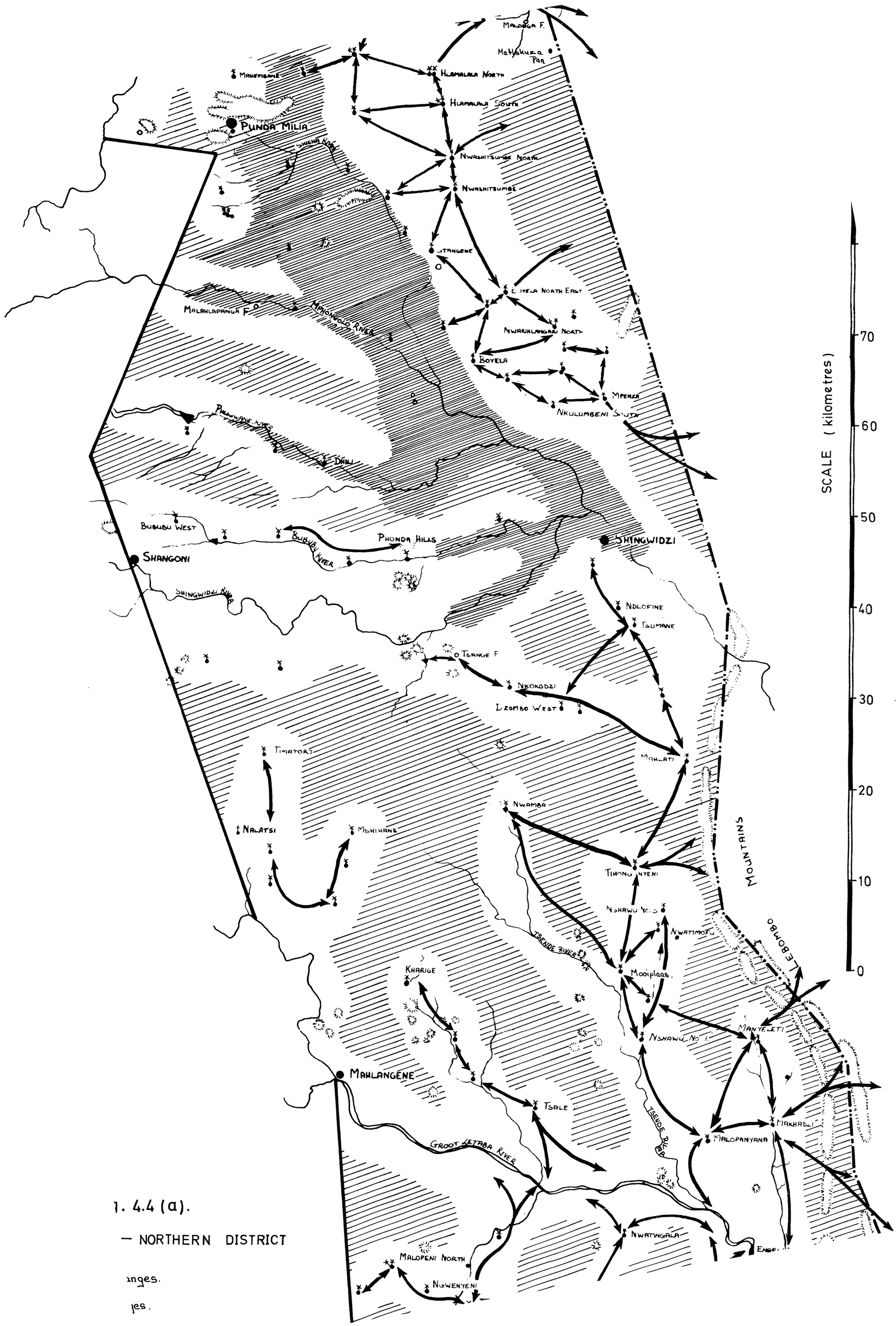
Basically the two sub-populations are separated from one another by an intervening belt of thick deterrent bush (Fig. 4.4.(b)) across which there are few traditional migratory routes. The southern boundary of unit (5) is formed by the Sabi and Sand rivers, while the northern boundary is again marginal zebra habitat, being mainly *Colophospermum mopane*/*Combretum apiculatum* woodland running up to the Olifants river. Unit (6) runs between the Sabi and Sweni rivers (north to south), its eastern boundary being the Lebombo mountain range.

4.3.1.2. Migratory direction, distance, routes and speed.

The seasonal migrations undertaken by zebra in units (5) and (6) are in a north-south direction, from winter to summer ranges and back (Fig. 4.4.(b)). As can be seen from this map the winter and summer grazing areas of both sub-populations are separated from one another by an intervening transitional zone. This zone may be utilized for a variable length of time, but the period is seldom more than a week or two.

Due to the size of both the winter and summer areas, the distance of the migration varies from year to year, the greatest

length,.../- 41 -



1. 4.4 (a).

— NORTHERN DISTRICT

anges.

ges.

i Steppe Forest (n.

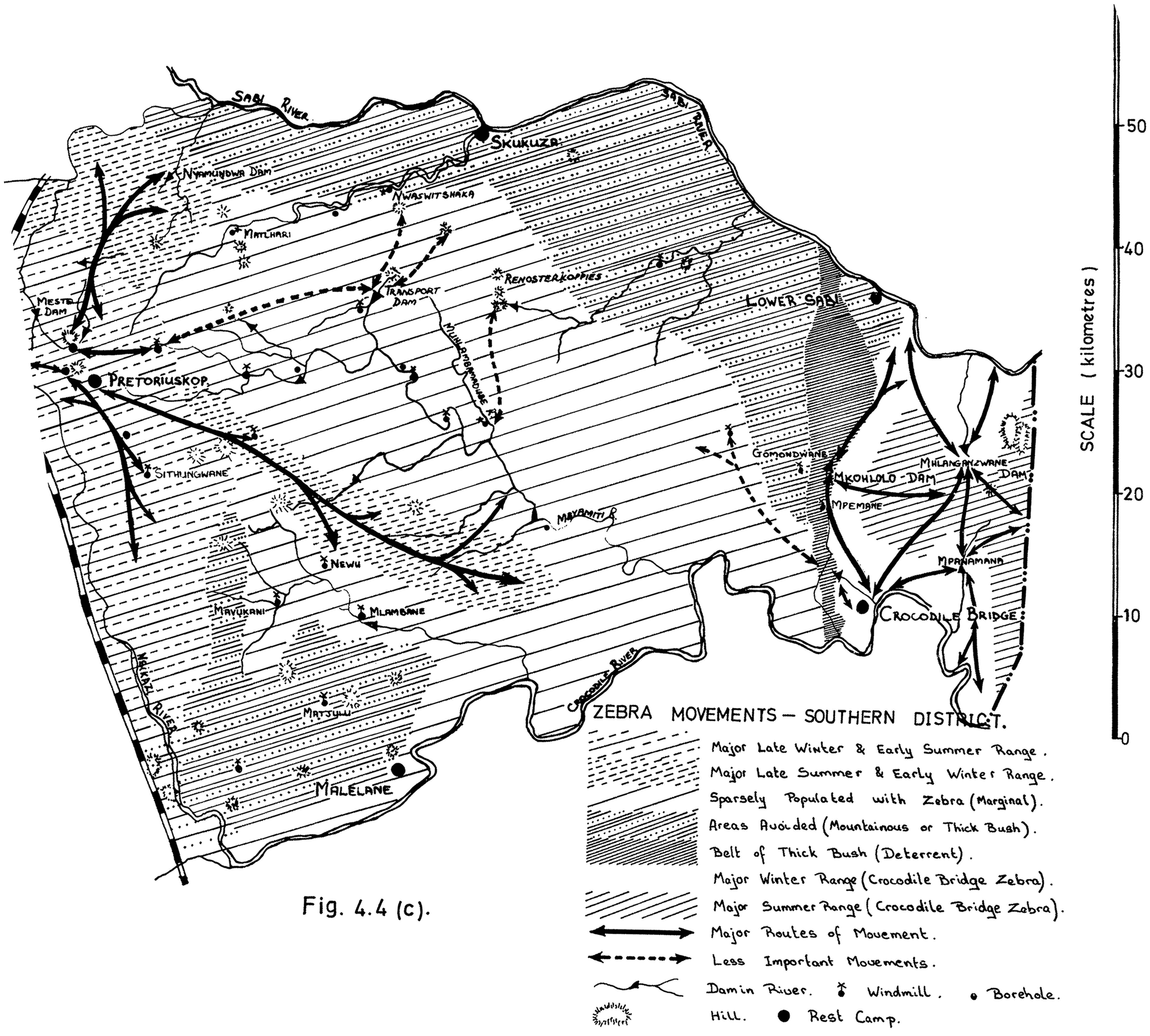

Sabi River
Skukuza
Sabi River
Nyamundwa Dam
Matlhari
Nwaswitshaka
Meste Dam
Transport Dam
Renosterkoppies
Muhlambanduwe
Pretoriuskop
Sithungwane
Mayamiti R.
Newu
Mavukani
Mlambane
Matjulu
Malelane
Nsikazi River
Crocodile River
Lower Sabi
Gomondwane
Mkohlolo Dam
Mpempane
Mhlanganzwane Dam
Mpanamana
Crocodile Bridge
SCALE (kilometres)
0
10
20
30
40
50
ZEBRA MOVEMENTS – SOUTHERN DISTRICT.
Major Late Winter & Early Summer Range.
Major Late Summer & Early Winter Range.
Sparsely Populated with Zebra (Marginal).
Areas Avoided (Mountainous or Thick Bush).
Belt of Thick Bush (Deterrent).
Major Winter Range (Crocodile Bridge Zebra).
Major Summer Range (Crocodile Bridge Zebra).
Major Routes of Movement.
Less Important Movements.
Dam in River.
Windmill.
Borehole.
Hill.
Rest Camp.

Fig. 4.4 (c).

length being 75 kilometres covered by eastern boundary zebra migrating between the Sabi river in the south and Milaleni windmill in the north (on the Sweni river). In contrast to this, the migratory zebra of the Etosha Salina (Ebedes, 1972) and those of the Serengeti region in East Africa (Grzimek and Grzimek 1960a and 1960b) undertake more extensive movements. In the Etosha Game Reserve zebra annually cover distances of between 100 and 160 kilometres, while in the Serengeti region the distances could exceed 200 kilometres. These distances refer to one way movements only and were calculated from maps provided by the authors previously cited. The movements of zebra in the Mara Plains region of Kenya (Darling, 1960) and in the Tarangire Game Reserve (Eastern Masailand) (Lamprey, 1964) are comparable again, in extent, to those of the sub-populations under discussion. Here the migrations appear to be between 50 and 80 kilometres in extent.

The distance travelled and routes followed by any migrating animal are correlated with its habitat requirements and the conditions prevailing at the particular time of the year. This is aptly illustrated when comparing the migration of African ungulates (tropical and sub-tropical) with those of Polar regions. The barren-ground caribou (Rangifer tarandus groenlandicus) for example, may at times cover distances in excess of 800 kilometres when moving from winter to summer ranges (Kelsall, 1970).

The routes followed by the migratory zebra of the central district are well defined and vary little from one year to the next. In the eastern boundary sub-population the route followed during the northward (spring) movement, however, differs from southward route.

When..../- 42 -

When moving northwards the greatest majority of these zebra swing towards the north-east and then follow the hills of the Lebombo mountain range until they reach their summer grazing area. When moving southwards at the end of the summer they remain, for the greatest part of the journey, on the Lebombo flats. This difference is not apparent on the west where both movements follow the same general route. The reasons for these differences will be discussed in Chapter 5. In all cases the routes followed are in the form of well defined paths which meander from place to place following the line of least resistance. When flying over these regions, especially the transition area, the paths traditionally used can be clearly discerned.

In most cases the speed of migration varies between four and six kilometres per hour, depending on the terrain. The type of locomotion may be described as a walk of medium speed similar to that observed when zebra move from one waterhole to another.

4.3.1.3. Seasonal timing of the migration.

Since the initiation of this study in 1969, three complete migrations, plus an additional southward one (1972), have been witnessed. These are summarised in Table 4.2.

Because the migrations of both the western and eastern boundary zebra take place at about the same time only the movements of the more important eastern boundary sub-population are given in the table.

Table 4.2. ..../- 43 -

Table 4.2.

Seasonal timing and duration of the northward and southward migratory movements of zebra in the central district of the Kruger National Park (1969 - 1972)

Year	Southward migration		Northward migration	
	Date when final large-scale migration was initiated	Time taken to reach winter range	Date when final large-scale migration was initiated	Time taken to reach winter range
1969	14th May	10 days	29th September	11 days
1970	30th January (± ½ of population) 3rd April (other half of population)	17 days 12 days	28th December	4 days
1971	26th May	5 days	16th October	6 days
1972	10th June	14 days	-	-

In many respects the data given in Table 4.2. are rather misleading and hence the unusual movements will be discussed individually.

Zebra utilizing traditional summer grazing areas are dependent for their water on veld pans, and pools in the seasonal rivers. Should these supplies be depleted they may be compelled to return to their winter range earlier than usual. When this occurs, the southward movement tends to be sporadic with only portions of the sub-population undertaking it. During the 1969/1970 season, for example, the spring rains were early and were followed by a comparatively dry summer (See Fig. 1.2.). On the 30th of January 1970, part of the sub-population migrated southwards and four marked

individuals..../- 44 -

individuals were seen at Mnondozi windmill on 17.2.70. However on 2.2.70 good rains fell in the northern part of the summer range and the remainder of the sub-population now concentrated in this area. They eventually only vacated the summer grazing area between 1 and 5.4.1970.

During the 1971/1972 summer when near record rainfall figures were registered throughout the Park (783,5 mm for the central district - April 1971 to March 1972), it again became clear that an unusual movement was going to take place. In contrast to a dry year, such as the 1969/1970 season, the summer range now had an abundance of water, while grazing conditions were excellent. Under these abnormal conditions (highest rainfall in more than 10 years) the zebra flourished, with the incentive to migrate consequently coming later than usual (Table 4.2.).

Comparing the southward migrations of 1969, 1970, 1971 and 1972 with those of 1966, 1967 and 1968 it appears that these movements are normally initiated during April or May.

With regard to the northward movements, sufficient rainfall is again essential and zebra will frequently initiate the migration, move a few kilometres and then again return to the winter range. This type of movement is continued until sufficient rain has fallen whence the migration is carried through. Should the initial spring showers be heavy enough, movements are not protracted and the migration is completed within two days. Exactly the same behaviour has been witnessed by Grzimek and Grzimek (1960a) in the Serengeti and these herds were also found to return in a westerly direction when there was a long break in the rains during the rainy season. A protracted northward

migration..../- 45 -

migration with a return to the original winter grazing area is less obvious on the west, since these zebra have a series of waterholes (both permanent and seasonal) along the greatest part of their route.

For the eastern boundary sub-population it is apparent that the duration of the northward movement is dependent on rainfall, good spring showers resulting in a rapid, less sporadic migration.

The time taken to complete a migration is difficult to assess since one would have to define a starting point and a finishing point. This is difficult, because the movement can end temporarily before such a point or be deflected round it by other more suitable conditions. In addition, one has thousands of animals to contend with and not merely a few marked individuals. The times given in Table 4.2. represent the duration of the migration for the greatest proportion of the population and not the times of one or two specific marked individuals. The time taken by selected individuals was found to be between one and two days in some cases. In East Africa zebra and wildebeest are known to move up to 40 kilometres in one night (Lamprey, 1964). These were migratory movements in response to local rainfall.

The initiation of the southward migration is not as sudden as the northward movement since the zebra are dispersed over a fairly large area where they utilize a number of different waterholes. When initially vacating the winter range, on the other hand, they are more concentrated, because of the almost exclusive utilization of water from the Sabi river and Mnondozi dam on the east, and Timbetene, Shiteve-teve and Sudweni windmills on the west. In addition to this, the stimulus to leave the winter range is a sudden one (rainfall) while that operating in the summer range is gradual (decreasing water

supplies..../- 46 -

supplies and/or poor grazing conditions). Due to this the influx of game onto winter ranges is also gradual and not quite as abrupt as that onto summer ranges. Similar observations have been made by Ebedes (1972), where zebra numbers were found to increase gradually on the Andoni Plain (winter range) north-east of the Etosha Salina.

Since northward migrations take place during or immediately after the first spring rains, the animals may subsequently move either by day or by night. Southward migrations take place during the cooler part of the day and also at night. While migrating, zebra move in single file, the family and stallion groups maintaining their individual identity. During these movements an adult mare customarily leads the migration, the adult stallion remaining at the rear of his group. Similar observations were made by Ebedes (1972). In most cases stallion groups remain towards the rear of migrating herds. While moving grazing is reduced, individual animals occasionally taking a mouthful of grass, but hardly stopping to do so.

4.3.1.4. Migration - instinctive or traditional?

Before migration can be broken down into its various phases one must decide whether the phenomenon is actually innate (instinctive) or whether it is, in fact, merely a seasonal reaction to proximate environmental conditions that has been passed on from generation to generation through the process of learning. In the last-mentioned case it would mean that years ago individuals or groups reacted to unfavourable conditions and so initiated a movement which eventually became traditional. This type of movement would, however, also require certain environmental stimuli for its initiation.

With regard..../- 47 -

With regard to the traditional or learnt, as opposed to the innate origin of migratory behaviour, it is difficult, in the case of mammals, to decide which is in fact the case. In invertebrates, especially insects, there is little doubt that migration is instinctive, as is much of their general behaviour (Lack, 1954; Smith, 1966). The North American monarch butterfly could serve as a classical example. This species migrates south in huge flocks each fall, roosting at night in selected trees. The return trip the following spring, however, appears to be made by the progeny of the autumn migrants, that apparently breed on the wintering ground (Beall, 1946). In the case of birds a similar instinctive situation exists and it has been proved conclusively, for example, that orientation or direction finding behaviour is independent of experience (Eibl-Eibesfeldt, 1970; Marler and Hamilton, 1966; Young, 1950). In these experiments birds were either hand-reared and then tested, or displaced from their normal course while busy migrating. In both cases directional responses remained correct.

In his book "The Migratory Springbucks of South Africa" Cronwright-Schreiner (1925) discusses the instinctive as opposed to the learnt origin of migration, and eventually comes to the conclusion that this behaviour is not instinctive in the springbuck. He postulates that their erratic movements were rather in search of food and possibly water, and because they did not occur annually, and were of variable direction, could not be regarded as true migration.

The erratic springbuck migrations which occurred in South Africa during the 18th century and those observed in the Kalahari during 1937, 1950 and 1954 (Brynard, 1956; Eloff, 1959) cannot, due to their temporal and directional irregularity, be regarded as true migrations.

These mass..../- 48 -

These mass movements and ensuing mortality, in fact, more closely resemble the "crash" migrations or irruptions of Arctic lemmings. Here, migration or rather emigration can frequently be correlated with social factors as the movement is often initiated before food becomes a limiting factor (Christian, 1963; Marsden, 1964).

Of the mammals today known to undertake migrations which are both regular and directional, the following diverse examples can be quoted: the fin whale (Balaenoptera physalus) (Laws, 1961); the hump-back whale (Megaptera novoengliae) (Davis and Golley, 1963); the little brown bat (Myotis lucifugus) (Davis and Golley, 1963); caribou (Kelsall, 1970); elk (Cervus canadensis) (Hamilton, 1939); mule deer (Odocoileus hemonius) (Taber and Dasmann, 1958); Thompson's gazelle (Gazella thomsonii) (Grzimek and Grzimek, 1960a); other African mammals have been mentioned in earlier chapters. From this it should be clear that migratory behaviour is not merely a phenomenon confined to a few species inhabiting a specific biotic zone, but that it is a relatively common occurrence in many diverse species all over the world. Considering the behaviour of all these species individually, and bearing in mind that instinctive migration is common in primitive groups such as insects, fishes and birds, one could postulate that mammalian migration is also instinctive, but, that it may be partially or completely suppressed in certain species. In this respect one may say that migration occurs in those species which survive in greater numbers if they leave, than if they remain in their breeding grounds for the non-breeding season (Lack, 1954) i.e. migration is merely an adaptation to the animals' particular environment.

In the..../- 49 -

In the case of mammals, the major factor contributing towards the belief that migration is not instinctive probably stems from the fact that many species are not migratory and within a species large proportions are completely sedentary, while others in neighbouring regions undertake a regular migration. This, I feel, should not defer one from the possible instinctive approach, since, after all, one of the basic traits of the higher mammals is their ability to modify behaviour through experience and learning (Manning, 1967). In this respect birds can again serve as an example. Winterbottom (1965) states that although many birds have an inherited tendency to fly in a certain direction, this tendency can speedily become modified. Here for example, the European starlings (Sturnus vulgaris) introduced into North America have lost their tendency to fly south-west in autumn and north-east in spring and do the opposite. The same species in the Western Cape does not migrate at all, but has reacquired the migratory habit in the summer rainfall area of the Eastern Cape. The same can be said for mammals. In South West Africa the zebra of the Etosha Salina migrate in a west-east direction while those in the Kruger Park, which are of the same subspecies, migrate in a north-south direction. Still other sub-populations are sedentary. In contrast to these deductions Watson (1966) feels that due to its sociality and reasonably long life, the migratory behaviour of the wildebeest could be passed on through learning (as a herd tradition).

Due to the present absolute lack of experimental data on mammalian migration, it would be impossible to decide whether the phenomenon is instinctive or traditional. The limited knowledge available, could in fact, be used to justify either of the two

possibilities..../- 50 -

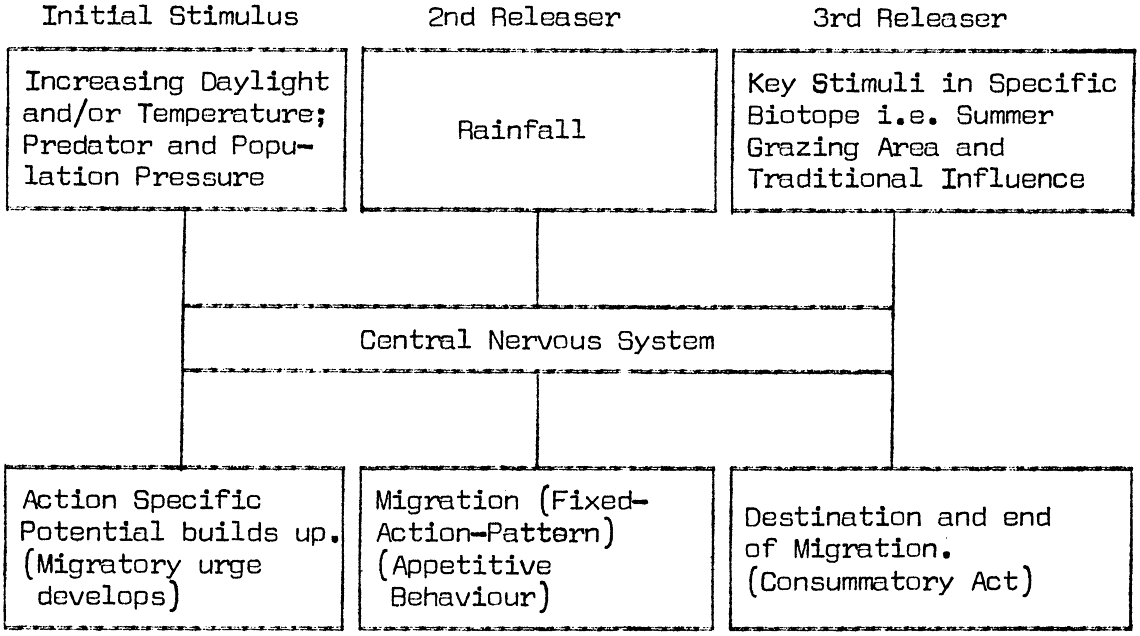
possibilities. Which one of the two is the correct approach, or whether the actual truth lies between the two, remains to be discovered, but it is abundantly clear that migration is a very plastic phenomenon which can be regulated to suit conditions.

4.3.1.5. Migratory restlessness and the stimuli involved in zebra migration.

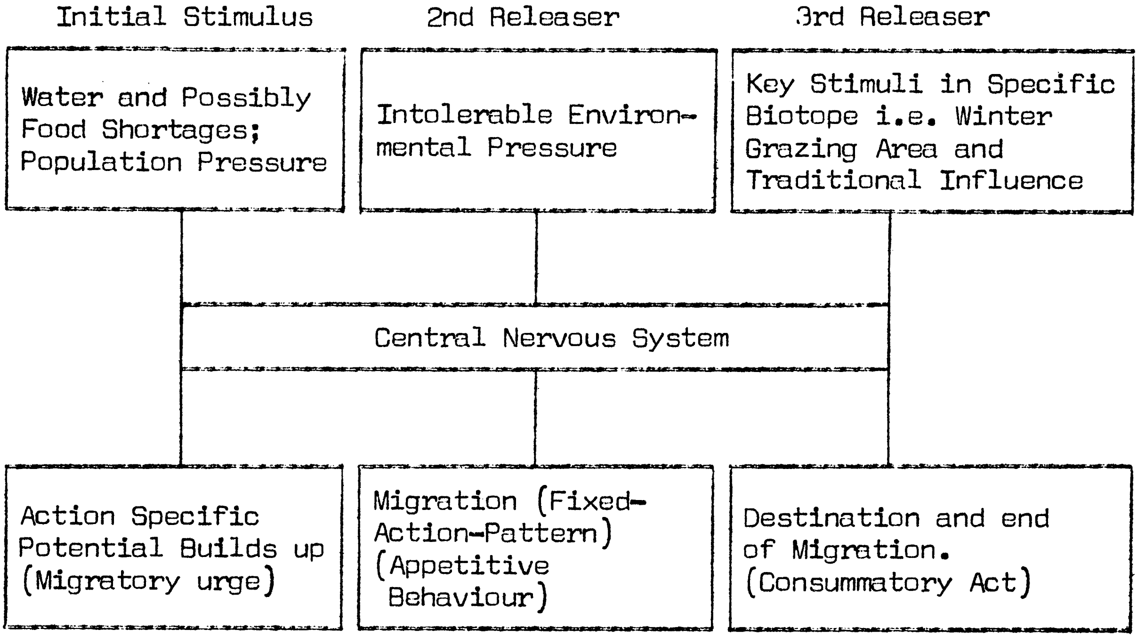
Accepting that zebra migration is possibly instinctive, a definition of instinct will help with the breakdown of migration into its various phases. Thorpe (1951) speaks of instinct as "an inherited and adapted system of coordination within the nervous system as a whole, which when activated finds expression in behaviour culminating in a fixed action pattern. It is organised on a hierarchical basis, both on the afferent and efferent sides. When charged it shows evidence of action-specific-potential and a readiness for release by an environmental releaser". Considering this definition and bearing in mind that all true migratory behaviour patterns will have a basic releaser-fixed action pattern system operating, one would expect the following phases to occur with respect to migratory zebra in the Kruger Park:

(i) northward..../- 51 -

(i) northward migration (central district)



(ii) southward migration (central district)



Considering the sections of diagrams (i) and (ii) individually, the following may be stated to justify the system:

(a) all..../- 52 -

(a) all northward migrations start after an initial period of increasing daylight hours and temperature (Fig. 1.2. and Table 4.2.). The relative % humidity data is inconclusive but it should fluctuate inversely with temperature (Griffiths, 1966). At this time of the year zebra also concentrate in increasing numbers round the remaining permanent waterholes and interspecific interactions (population pressure) may also be part of the initial stimulus. These factors are responsible for the build-up of action-specific-potential and the initiation of the migratory urge. The importance of the photoperiod in initiating migratory behaviour in birds (Smith, 1966; Winterbottom, 1965) and fish (Marler and Hamilton, 1966) is well known. Similarly, temperature is known to play a role (Smith, 1966; Kendeigh, 1961). In mammals, as in birds, the length of day and night, and temperature also have important influences on the oestrus cycle and sexual behaviour (Amoroso, 1955). In mares, for example, Burkhardt (1947) has shown that oestrus and ovulation followed by pregnancy could be induced in anoestrous mares by general irradiation with strong artificial light. Since light and temperature are significant in initiating migratory behaviour in birds and important in the sexual activities of many mammals (especially those of the temperate zones) one could advance a similar link between these factors and mammalian migration. This is, however, a mere postulation that would be extremely difficult to verify experimentally,

(b) as soon as the first spring rains fall (2nd releaser) zebra mass together in herds of up to 300 or more. Occasionally wildebeest and zebra herds mix but to a large extent they retain their identity. During this initial massing both species are extremely active. They run about in circles, kicking up the hindlegs and pawing the ground.

Zebra..../- 53 -

Zebra frequently bite and kick each other or simply jump about on one spot. Attempted copulations and vocalizations are also more frequent than ususal. During this period of increased motor activity, feeding is reduced or non-existent and the animals tend to orientate themselves in a northerly direction. Eventually the migration starts with a number of groups setting off together. Later, however, the migrating animals form the extended files previously described. The initial congregating activity is very common in birds (Winterbottom, 1965), especially swallows, but is seldom seen in mammals. Migratory restlessness and massing of herds of zebra and wildebeest have, however, been witnessed in East Africa (Lamprey, 1964). Since this activity only lasts for a short time with mammals, usually occurs in fairly isolated areas during unpleasant weather, and only occurs on one or two days during the year, one could hardly expect it to be seen very frequently. In addition, depending on the distribution of game before the first rains, the phenomenon may be less obvious during successive years,

(c) another parallel that can be drawn between birds and zebra is that they will only respond to a stimulus to migrate if that stimulus reaches a certain minimum intensity ("threshold"). In section 4.3.1.3. it has been mentioned that zebra of the eastern boundary subpopulation frequently initiate the northward migration, but then again return to the winter range. This up and down, or recirculation movement in the summer grazing area (Fig. 4.4.(b)) is continued until sufficient rain has fallen, whence the migration is carried through; i.e., once the threshold level, which is determined by rainfall, has been exceeded, the migration is completed. This movement could be explained on the basis of instinct, i.e. a fixed neural pattern

exists..../- 54 -

exists which requires a certain minimum intensity (theshold) before it fires. It could, however, also be justified by the traditional approach i.e. the animals know (remember) that should they complete the northward movement they may have water and/or food shortages to contend with when they reach their summer range. Because of this, they delay the movement until sufficient rain has fallen.

The more sporadic type of movement observed during the southward migration can similarly be explained on the basis of "threshold". Here, the sub-population tends to be more dispersed, with some herds possibly drinking and grazing in the Sweni area, while others may be drinking at Mazithi dam or in pans on Lindanda some 16 or more kilometres away. During January 1970, for example, there were water shortages on Lindanda and the majority of the zebra that were then drinking at Mazithi dam migrated southwards (Table 4.2.). Those, however, that were in the Sweni area did not experience these water shortages and on 2.2.1970 excellent rain fell in this region. These zebra, in fact, only migrated south to Mnondozi on 3.4.1970, some two months after the first group. This example serves to illustrate how water shortages eventually become intolerable, reach the minimum intensity and hence initiate the fixed-action-pattern (migration).

During 1969 extreme food shortages on the western boundary was believed to be the prime factor in initiating the southward migration of these zebra. It is interesting, however, to note that zebra always leave their summer range before water supplies have been depleted. This was especially obvious in the autumn of 1972 when zebra in the Lindanda area started moving southwards during the first half of June. At this stage water was still abundant in the summer grazing

area,..../- 55 -

area, and the range was in fair condition. The fouling of water may also play a role in stimulating the movement (Swynnerton, 1958). Watever the stimuli involved in initiating the southward movement, it is clear that during exceptionally wet years these are suppressed and one has a more sporadic migration which takes place later than usual e.g. the late southward migration witnessed during 1972 (Table 4.2.).

(d) supporting the supposition that the fixed-action-pattern of migration is accompanied by simultaneous appetitive behaviour, is the fact that zebra captured while migrating, or just after reaching their summer ranges, inevitably injure or kill themselves when placed in enclosures. During 1969 and 1970 zebra used to be captured on a daily basis in the central district of the Kruger Park. Usually three to five animals were captured per day by using conventional immobilizing drugs and tranquillizers. After capture, the animals were crated and then transported to comfortable bomas at Tshokwane. It soon became clear that during migratory periods mortality at the bomas rose phenomenally as aniamals either broke their necks while attempting to escape or had to be destroyed due to injuries sustained in their frantic attempts to clear the stockade wall. In some cases zebra even broke out of their crates while being transported, either by kicking down one of the doors or jumping through the roof. This phenomenon was serious enough to hamper capture programs for a week or two per year.

When observing the penned migratory zebra it was clear that they were extremely restless and that they behaved quite differently to those captured some time after or before the migration,

(e) how do..../- 56 -

(e) how do zebra know when they have reached their goal or destination? The movements of individually marked specimens have shown that the same animals tend to return to the same general area year after year. The fact that zebra, expecially those on the east, do not overshoot their mark must mean that they can recognize their summer range, since they could quite conceivably continue this movement and still find very suitable grazing areas north of the Sweni river. Key stimuli must therefore play a role in the recognition of winter and summer ranges.

Should zebra, migrating northwards, reach the Lindanda area and find that the grasses have not sprouted sufficiently to support their grazing requirements, they continue northwards towards the Sweni, with many also congregating along the Makongolweni spruit. During normal years, on the other hand, most of these animals remain in the Lindanda area and may only move towards the Sweni after a month or two, or not at all. The initial movements across Lindanda are due to the absence of suitable stimuli, the animals thus continuing their search further northwards. Fig. 4.5. gives one an idea of what Lindanda looks like when key stimuli are lacking and shows a herd of migratory wildebeest actually crossing the traditional summer range and moving towards the Sweni area.

4.3.1.6. The beneficial aspects attributable to zebra migration.

In contrast to sedentary zebra such as the Satara subpopulation, the migratory zebra of the central district are benefited by undertaking these movements in the following ways:

(a) by complete rotational utilization of summer and winter

ranges..../- 57 -

Fig. 4.5. With key stimuli lacking in the traditional summer range, a herd of wildebeest migrate across the Lindanda plains in search of better grazing to the north, December, 1970.

ranges they are able to take maximum advantage of the food provided by an area that is only seasonally habitable. This complete rotation is not as obvious in sedentary populations. The rotational system also allows the heavily grazed winter ranges to recover completely and affords partial rest to summer ranges,

(b) by leaving summer and winter ranges at the appropriate times they avoid social strife associated with inter- and intraspecific competition. Sedentary populations are less successful in this respect.

4.3.1.7. Some comparisons between the migratory movements of zebra and wildebeest.

Comparing the migration of zebra and wildebeest the following should be noted:

(i) in the western boundary area the northward and southward movements of both species are fairly similar. The wildebeest are, however, inclined to utilize the summer grazing area for longer periods than the zebra. Zebra consequently move southwards before the wildebeest,

(ii) in the eastern boundary area very few wildebeest penetrate the Lebombo hills during their northward movement. They remain instead on the Lebombo flats, the greatest majority migrating northwards via the same route used by the zebra when migrating southwards. Lone bulls are the first animals to reach the summer grazing areas. As is the case on the west, the wildebeest leave the summer range after the majority of zebra have migrated.

4.3.2. Semi-migratory sub-populations.

The following four semi-migratory sub-populations have been discerned:

(a) zebra..../- 58 -

(a) zebra between the Levubu and Shingwidzi rivers (Fig. 4.3, Unit (1)),

(b) zebra between the Shingwidzi and Letaba rivers (Fig. 4.3, Unit (2)),

(c) Crocodile Bridge zebra (Fig. 4.3, Unit (8)),

(d) Pretoriuskop, Malelane, and Skukuza zebra (Fig. 4.3, Unit (7)).

4.3.2.1. Discussion of the boundaries and barriers between these four sub-populations and others.

These sub-populations are regarded as being semi-migratory because the distances which they move are considerably less than those of sub-populations (5) and (6). Additionally these movements are not as strongly directional as those of the migratory zebra and there is no comparable mass movement. With the exception of sub-population (7) these zebra could be better described by using the term "opportunity migrants", since migratory behaviour may not take place or be protracted during very dry years.

The northern boundary of unit (1) is formed by the Levubu river and the southern boundary of unit (2) by the Letaba river, which occasionally flows throughout the year. In both areas the western boundary is a game deterrent fence and the eastern boundary the Lebombo mountain range.

In the Crocodile Bridge section (unit (8)), the northern and southern boundaries are again formed by perennial rivers, while the eastern boundary is the dry Lebombo ridge. Areas (7) and (8) are separated by a continuation of the belt of mixed thorn bush from the

central..../- 59 -

central district (Fig. 4.4.(b) and (c)) and marginal zebra habitat on its north-easterly side (see also Fig. 1.3.). The other boundaries of unit (7) are formed by the Sabi and Crocodile rivers and the western boundary fence.

Further division of zebra in areas (1) and (2) is possible on the basis of vegetation composition and hence soil type. Here the greatest concentrations are found on the basaltic soils of the Lebombo flats - some 1900, while only 1300 inhabit the soil types to the west of the sandstone reef (Fig. 1.1. and 1.3.). The more westerly zebra are sedentary by nature, their seasonal movements entailing a general summer dispersion away from the permanent waterholes to the hilly water sheds of rivers such as the Shisha, Mphongolo, Phugwane, Bububu, Shingwidzi, Tsende, Byashishi and Shipikane.

Zebra in the western part of area (1) are separated from those of the Lebombo flats by a belt of climax *Colophospermum mopane* forest. This forest belt runs along the Shisha river down to Shingwidzi camp and on the alluvial soils of tributaries of the Shingwidzi river (Fig. 1.3.). In unit (2) a similar situation exists because of the thick *Colophospermum mopane* bush on the western side of the Tsende river.

4.3.2.2. Discussion of the movements undertaken by zebra to the east of the sandstone reef, in units (1), (2) and (8).

During years of good rain the habitat of zebra in units (1), (2) and (8) may be divided into fairly distinct winter and summer grazing areas, lying side by side. Here the summer grazing area is the well drained soils of the Lebombo mountain range, while the winter area

is the..../- 60 -

is the adjacent Lebombo flats. During dry years, on the other hand, few zebra move towards the east and the summer grazing area now forms a mosaic pattern around the winter grazing areas - similar to the situation in the sedentary Satara and Letaba sub-populations (Fig. 4.4. (a) and (b)).

The movements of zebra in unit (7) will be discussed separately in section 4.3.2.3.

During the dry winter months zebra in units (1), (2) and (8) spend most of their time in the vicinity of permanent waterholes seldom moving more than two or three kilometres from the nearest waterhole. Winter movements in excess of about six kilometres usually entail the movement from one waterhole to the next. (This six kilometre distance refers to a straight line between the animal and the waterhole and not to its meandering walking pattern).

During good summers the movements of the more easterly zebra in units (1), (2) and (8) are generally very similar, being from west to east. Few zebra in unit (8), however, appear to undertake the eastward movement and fair numbers instead move onto the higher ground to the west and north-west of Crocodile Bridge camp.

When conditions are dry during the summer months zebra in the above three areas are compelled to utilize the permanent waterholes on the Lebombo flats due to the scarcity of water to the east.

Fairly significant eastward movements away from the Park are witnessed in the north-east between the Shilahlandonga river, Machayi windmill and Matlakuza Pan. During good summers numbers of zebra from the Hlamalala- Nwashitsumbe region of the Lebombo flats leave the Park via this route and move into the hilly *Colophospermum mopane* shrub

savanna..../- 61 -

savanna to the north-east. It is believed that zebra move as far east as the catchment area of the Mafufunyane spruit in neighbouring Mocambique, the habitat being a continuation of the hilly mopane shrub and tree savanna (Joubert, 1970). Small groups also enter open parts of the Nwambia sandveld (see vegetation map) both inside and outside the Park. This rather dense deciduous scrub with scattered trees is found on the deep well drained red sands of a Kalahari-like origin. Similar eastward movements and possibly some emigration is believed to occur from the shrub mopane savanna woodland south-east of Mpenza windmill (Unit 2). In these areas as well as those to be discussed below, it is important to remember that summer shifts are totally dependent on rainfall both in their intensity and duration. During dry years such as 1969/1970, dispersion is very local with few, if any, of the zebra moving beyond the eastern boundary of the Park. They then also return to the Lebombo flats earlier than usual.

Possibly the most noticeable zebra movements occur from the region between Tihongonyeni and Malopanyana windmills (unit (2)). This region (Klipkoppies section) houses a population of some 1200 zebra, the factors influencing their movements being similar to those of the Hlamalala- Nwashitsumbe area. Zebra from this section fortunately do not have to move far towards the east to find the summer conditions they prefer, since the Lebombo hills stretch further into the Park in this region than anywhere else (Fig. 4.4.(a)). The type of habitat evacuated during the summer months and the sudden change in altitude between the Lebombo flats and the Lebombo mountains can be gleaned from Fig.4.6. and Fig. 4.7.

In contrast..../- 62 -

Fig. 4.6. Typical habitat evacuated by semi-migratory zebra of the northern district during the wet season. Notice the small Colophospermum mopane shrubs typical of large areas. Lebombo flats near Manyeleti dam, February, 1971.

Fig. 4.7. The Lebombo mountains (background) just east of the Lebombo flats (foreground). Portions of these hills are important wet season ranges for the zebra of the Lebombo flats. Manyeleti dam area, February, 1971.

In contrast to these typical eastward movements witnessed during years of good rainfall, the zebra in the Satara area are less inclined to undertake this movement. The reason for this difference lies in the habitat to the south-east of the Olifants river. Here portions are either inaccessible to zebra or so dense as to be completely avoided. Areas such as exist just north and south of the Pumbe sandveld (Fig. 1.3.) are however utilized by small herds during the summer months.

The rugged terrain on the east of the Park, together with factors such as dense vegetation and the few zebra that were marked in the north, make further conclusions difficult. It is hoped that uncertainties with regard to movements in this area will be elucidated by a future marking program, especially with an eye on the proposed eastern boundary fence.

4.3.2.3. Discussion of the movements undertaken by zebra in unit (7).

Zebra in the Pretoriuskop, Malelane and Skukuza sections (Fig. 4.3. unit (7)) are unique in that their movements differ quite markedly from those in any other region of the Park.

These zebra exhibit a basic movement which in many respects could be called a migration. The movement is, however, insignificant when compared to the central district, since it is undertaken by small herds and individual groups which converge onto the same general area. The time of arrival and departure of these herds are by no means synchronised and there may be differences of up to two months. In addition to this the average dates when these movements occur are quite different from those of the true migratory zebra, or from that of any other subpopulation.

The movements..../- 63 -

The movements duly to be discussed refer to the bulk of the population which seasonally utilize the grassland of the Pretoriuskop area, and not to the groups to the north-east of the Hlambamaduba and Mbyamiti rivers. These last mentioned zebra tend to wander about in groups and small herds, utilize marginal habitat and undertake very local movements. This, together with their insignificant numbers (200-300), precludes further discussion of their movements.

When looking at the map on the movements of zebra in unit (7), (Fig. 4.4., (c)) it is clear that seasonal movements occur between the Terminalia sericea/Dicrostachys cinerea subsp. nyassana savanna woodland with tall grass of the Pretoriuskop area and the Acacia nigrescens/Albizia harveyi savanna woodland to its east (Fig. 4.4.(c) and Fig. 1.3.). When analysing these movements it is found that the seasonal ranges may be divided into:

(i) an area utilized throughout the year yet mainly during the late winter and early summer. This area comprises a large portion of the Pretoriuskop savanna woodland with tall grass area (Fig. 4.4.(c) and Fig. 1.3.),

(ii) an area utilized during the late summer and early winter. This area, to a large extent, follows the doleritic soil belt which runs through the region from north to south and then sweeps eastwards (Fig. 4.4.(c), Fig. 1.1. and Fig. 1.3.).

The movements of zebra within and between these two seasonal ranges are regulated by factors such as the biannual rotational burning program, the topography and the availability of surface water. These factors are discussed in chapter 5.

4.3.3. Sedentary..../- 64 -

4.3.3. Sedentary sub-populations.

The two sub-populations regarded as being sedentary are:

(a) the Letaba zebra (Fig. 4.3., Unit (3)),

(b) the Satara zebra (Fig. 4.3., Unit (4)).

4.3.3.1. Discussion of the boundaries and barriers between these two sub-populations and others.

These two units are unique in that the zebra of both sub-populations undertake seasonal movements of a very localized nature. These movements take place in any direction depending on the condition of the surrounding veld and may be defined as local movements from the immediate vicinity of permanent waterholes to surrounding under utilized areas.

Zebra in unit (3) (Letaba) have the Olifants and Letaba rivers and the western boundary fence as borders. Those of unit (4) have the Olifants river in the north, the Lebombo mountain ridge on the east, the Timbavati river and the belt of thick thorn forest on the west and Sweni river in the south, as their borders. Although the Sweni river only flows for a few days each year, it is surprising how few of the Satara zebra cross this boundary. Of some 20 zebra marked in this region, two crossed the Sweni, but both later returned. Zebra from unit (6) seldom move more than a kilometre north of the Sweni river and always join up with the migratory herds when they move south.

4.3.3.2. Discussion of the movements undertaken by zebra in units (3) and (4).

In these regions the summer grazing areas form a mosaic pattern around the winter grazing areas (Fig. 4.4.(a) and (b)) and

are not..../- 65 -

are not separated as in migratory sub-populations by intervening transitional areas.

Daily winter movements between grazing areas and permanent waterholes are similar to those previously described for semi-migratory sub-populations during the winter season, while summer movements in the summer grazing areas are even more localized, the animals occasionally moving to another area, depending on conditions. These daily movements take place within the home range of the particular group, which always encompasses both suitable summer and winter areas. Here movements usually occur on a small scale (one to 50 animals) and all the animals in a particular area do not mass together before they leave - some may remain behind while some depart, and others possibly arrive. The only consistency with regard to local movements (while in winter or summer grazing areas) is in fact the irregularity of such movements.

Chapter 5..../- 66 -

Chapter 5

FACTORS AFFECTING THE ZEBRA'S CHOICE OF HABITAT, DISTRIBUTION, MOVEMENTS AND MIGRATION.

The multitude of factors which individually or collectively influence or determine the spatial distribution, local movements and migration of the various zebra sub-populations will be discussed in this chapter.

Although zebra may be regarded as a species with tremendous adaptive flexibility, they nevertheless have a definite choice of habitat. The daily and seasonal movements which they undertake prove that they are reacting to some unfavourable habitat condition, instinctive urge, or that they know where better conditions exist. Leopold (1969) states that the adaptability of many species depends not only on their genetic plasticity but also on their capacity to learn and consequently to adjust their behaviour in accordance to the altered environmental conditions. In this respect all species are not as fortunate as the zebra i.e. they are less flexible to, or tolerant of, the altered conditions. The present status of the roan antelope, the sable antelope and the tsessebe in the Kruger National Park serve as adequate examples of how three species are struggling, in certain regions, to adapt themselves to a changing environment. In contrast to the zebra which is capable of utilizing subclimax or climax grass communities, these species thrive only on the climax grasslands where they can satisfy their selective habitat requirements. Similar examples are quoted by Leopold, (1969) for a number of North American ungulates.

Here species..../- 67 -

Here species such as caribou (Rangifer arcticus), bighorn (Ovis canadensis), mountain goat (Oreamnos americanus) and bison (Bison bison) are associated primarily with climax forage types, while species such as moose (Alces americana), elk (Cervus canadensis), white-tailed deer (Odocoileus virginianus) and mule deer (Odocoileus hemonius) are associated primarily with subclimax forage types.

5.1. Water.

Although vegetation type is one of the most important factors governing an animal's selection of a particular habitat (Dice, 1952), water is in many instances equally important both physiologically and ecologically (Young, 1970). Not only does the availability of drinking water limit the density obtained by species in a particular area (Dasmann, 1964), but should it be absent, either temporarily or permanently, water dependent species will to a large extent not be able to utilize the area.

When contemplating the possible effects which drinking water can have on game distribution and movement, it is essential not only to consider its mere availability, but also its chemical composition. In the Etosha National Park, for example, the water in six permanent waterholes from a sample of 19, tested during the dry season, was found to be unsuitable for game use. The reason for this was a high increase in the salt and alkaline content. Here it is believed that the continual intake of highly saline water together with the eating of halophytic grasses has an adverse and detrimental effect on the normal physiological functions of the body and that zebra instinctively move away to areas where fresh grazing and drinking water is available (Ebedes, 1972).

The chemical..../- 68 -

The chemical analysis of water samples taken from almost 150 boreholes and springs throughout the Kruger Park (Young, 1970) has shown that although certain components occur in a rather high concentration, the water is still utilized by zebra. In certain cases waterholes with high concentrations of salts may be actively selected. Zebra and other game have on occasions been observed to drink from highly saline veld pans in preference to neighbouring fresh water pans (Young, pers. comm.).

In certain regions of the Kruger Park water is a limiting factor to the distribution of zebra. This factor is however, largely confined to the winter season and unusually dry years. Considering the water requirements of the species it is clear that they require water almost daily. According to Shortridge (1934), Hartmann's zebra Equus zebra hartmannae does not drink regularly; Burchell's zebra, however, does (Buckley, 1876; Stevenson-Hamilton, 1947) and in the Kruger Park they have been found to drink 1,5 times per 24 hours during the summer and on an average once every 35,2 hours in winter (Young, 1970). The more regular drinking periods during the wet season are largely due to the greater abundance of watering points at that time of the year.

The dependence of zebra on surface water can also be gauged when studying the "cruising radius" or mean daily distance which they move away from a watering point. Young (1970) found that the average daily "cruising radius" of zebra herds during summer and winter was 3,41 kilometres and 7,68 kilometres respectively. These distances are however, not only determined by the water requirements of the animal, but also by the condition of the veld surrounding the particular

waterhole..../- 69 -

waterhole (van der Schijff, 1957 and 1959). Distances in excess of eight kilometres usually entail movement from one waterhole to the next, rather than a true "cruising radius".

As soon as the first spring rains fall, zebra herds in sedentary sub-populations disperse into previously underutilized areas. This movement is not always due to a lack of adequate grazing round the permanent waterholes, but due to the fact that they prefer to drink from natural veld pans. Many permanent watering points are in the form of cement troughs and Young (1970) has proved that zebra prefer earth dams and veld pans to these artificial troughs - provided the water is not too muddy. At Sundweni windmill, west of Tshokwane, where a cement trough and a small veld pan are only about 15 metres apart the obvious choice of zebra for the pan can be clearly seen - few if any of the animals utilizing the trough while there is water in the pan.

As is the case with most game animals, especially elephant, zebra often dig holes in dry river beds to find water (Fig. 5.1.). These holes, which are commonly found during times of drought, are excavated with the hooves of the fore-legs and may be dug by the zebras themselves, or they may utilize those made by other animals. Zebra, in common with most game species, prefer clear water to murky or fouled water and will consequently wade a short way into a pan or dam, or stretch their heads forwards to get at the better water away from the edge. (Fig. 5.2.). They do, however, show a reluctance to enter the water of large dams, but this fear is significantly suppressed when in large herds. Under these conditions they may even enter up to the level of their bellies.

When the..../- 70 -

Fig. 5.1. A zebra drinking water from a hole it had excavated in the bed of a seasonal river. Nwanetzi, July, 1969.

Fig. 5.2. Zebra either wade a short way into dams or stretch forwards to get at the cleaner water away from the edge. In this respect they are more reluctant to enter water than are wildebeest. Nwatindlopfu, July, 1969.

When the Lugmag dam in the central district was almost empty and rather muddy, zebra were seen to dig drinking holes in the sand, two or three metres away from the edge. They drank from these holes in preference to entering the water. Wildebeest in contrast, readily waded into the dam to drink.

Because of their dependence on water, zebra are frequently compelled to utilize overgrazed areas around permanent waterholes. However, once substantial rain has fallen in the surrounding area they immediately leave. As soon as the water in neighbouring veld pans commence drying up and become muddy, they again return to the permanent waterholes. Wildebeest, in contrast, readily drink muddy water and only leave when there is absolutely nothing to drink. This phenomenon has been observed on a large scale in the summer grazing area along the Sweni river. In the Nyai Pan area situated north of the Makarikari Pan in Botswana, which is the wet season grazing area of large herds of zebra and wildebeest, Birkenholz (1967) found that zebra left the pan and migrated southwards as soon as water supplies dwindled. Wildebeest, on the other hand, were found to linger for several weeks without water, provided fresh grass was available.

5.1.1. The effects which the drinking habits of zebra have on their movements and the habitat.

By studying the habits of the migratory zebra of the central district, it will be possible to illustrate the vital role played by water in determining the utilization of available grassland.

Natural watering points in summer grazing areas are usually of a temporary nature, seldom lasting for any length of time into the

winter..../- 71 -

winter. They are also normally in the form of natural veld pans, or pools in the seasonal rivers. The normal state of affairs in these areas is that the seasonal pans commence drying up towards the end of the summer, the game consequently returning to their winter ranges which have permanent water supplies. Should permanent water be supplied in summer grazing areas, game such as zebra and wildebeest are inclined to remain in these areas longer than usual with the result that portions of the range may become overgrazed and trampled. In the Kingfisher-spruit area, for example, where permanent water was supplied (Chapter 2 sections 2.2.1.), the habitat has been badly degraded. This in turn has resulted in a retrogressive succession, with parts of the habitat being almost denuded of grass. The dominant grasses are presently mostly pioneer annuals such as *Tragus berteronianus* and *Urochloa mosambicensis* with associated annuals such as *Pogonarthria squarrosa* and *Aristida curvata* (Gertenbach and Nel, pers. comm.). In the past (prior to 1960) the grass cover consisted of a mixed sweet veld where *Themeda triandra*, *Digitaria* spp., *Cymbopogon excavatus* and *Heteropogon contortus* were dominant with *Eragrostis superba*, *Panicum maximum*, *Brachiaria* spp., *Urochloa* spp., *Cenchrus ciliaris*, *Hyperthelia dissoluta* and *Eustachys paspaloides* as associated species (Pienaar, 1965). In conjunction with the retrogressive succession experienced in the grass community, there has also been a simultaneous increase in the woody growth. The successional changes which have taken place in this area are, however, not only due to the provision of permanent water, but, also to a reduction in the size of the summer grazing area by the western boundary fence.

In the..../- 72 -

In the summer grazing area of the eastern boundary zebra, a similar, yet less alarming situation exists. The reason for the overgrazed condition of this habitat is described in chapter 2 section 2.2.2. Here,by tampering with the natural rotational grazing system, which is largely regulated by water supplies, the basal cover in portions of the range has been reduced to less than 3,5%. In the corresponding winter range round Mnondozi dam and Rietpan, where the habitat has ample time to recover during the growing season, the basal cover is over 6,0% (Gertenbach and Nel, pers. comm.). The wheelpoint method of Tidmarsh and Havenga was used in these experiments.

As mentioned in chapter 4 section 4.3.1.2., the southward migration route of the eastern boundary sub-population differs from the northward route. This difference could partly be due to water shortages in the Lebombo hills towards the end of the summer. On the western boundary the paths of zebra migrating southwards follow the chain of permanent waterholes which link summer and winter ranges. A similar situation exists in the Etosha Game Reserve where zebra migrate round the Salina in an anticlockwise direction. Here the return movement to the dry season range follows the southern part of the Salina which is well supplied with permanent waterholes (Ebedes, 1972).

Due to the excellent series of resightings obtained on marked zebra in the central district (over 70 per animal in some cases) it has been possible to analyse their yearly drinking habits with some accuracy. Utilizing this data it has also been possible to compare the drinking habits of sedentary and migratory sub-populations. This

comparison..../- 73 -

comparison has shown that differences can largely be ascribed to the fact that the winter ranges of migratory zebra have fewer watering points than the corresponding ranges of sedentary zebra. During the course of the dry winter months, for example, the sedentary Satara zebra utilize between three and five waterholes within their home range (mean = 4). During this time they seldom spend more than a week or two in the vicinity of a particular waterhole - usually they spend shorter periods, and then move to another. At times they may move backwards and forwards between two waterholes and then suddenly move to another. In contrast to this, the migratory sub-populations usually only have two or three permanent waterholes at their disposal. During very dry years the eastern boundary sub-population may drink exclusively in the Sabi river and at Mnondozi dam. Particular groups may utilize one of these watering points for periods of up to three months or more. Should this winter grazing area have received good summer rains the zebra and wildebeest avoid the normal permanent waterholes such as Mnondozi dam and Mnondozi windmill and drink almost exclusively from veld pans, or pools in the seasonal rivers. During the 1970/1971 season, for example, the traditional winter drinking points of the eastern boundary zebra were almost totally avoided, veld water being plentiful in the surrounding area. The winter drinking behaviour of the Satara zebra, which have a network of waterholes at their disposal, and that of the eastern boundary zebra during years of very good rainfall thus shows that zebra prefer to drink from a number of waterholes. The network available to the Satara zebra thus accounts, to a large extent, for their sedentary habits, as they are able to escape inter- or intra-specific competition and predation by moving

to another..../- 74 -

to another waterhole.

Although the availability of drinking water has its greatest regulating effect on the movements of zebra during the dry season, it may have similar effects during the summer. On the 23rd of November 1971, for example, the block between Ngirivane windmill, the Timbavati river and the Orpen/Satara roads was burnt. Prior to this date rainfall in the area had been sporadic, and in the form of light showers, with a total of 17,5 mm and 24 mm being registered for October and November respectively. These showers were all betweeen four and eight millimetres and hence not sufficient to fill any veld pans or seasonal streams. The grassland, however, reacted favourably and by the end of November it was in excellent condition. At this stage there were almost no zebra or wildebeest in the area and only odd groups or solitary animals were noticed. Since the soil was fairly moist by this time, the good rain which fell on 7.12.71 (over 20 mm) soon filled streams and veld pans. By 14.12.71 (possibly sooner) large numbers of zebra had moved onto the fresh grass of the burn. Three marked individuals resighted, indicated that most of the zebra had moved in from the Mtomene windmill area about 16 km to the north-east. By the end of February veld water was depleted and although the grazing was still good, most of the zebra had again left.

5.2. Feeding behaviour and grazing conditions.

Of the factors regulating the distribution and movements of zebra, the condition and availability of forage is of great importance. Provided drinking water is present and the factors to be mentioned in the following sections of this chapter are acceptable, proximate

grazing..../- 75 -

grazing conditions will directly determine distribution patterns and local concentrations.

With a knowledge of the feeding behaviour of zebra it will thus be possible to make a number of deductions with respect to the effect of grazing conditions on movement patterns and consequent changes in distribution. The effects of fire, rainfall and grazing intensity will also be considered in this section, since these factors, to a large extent, create the grazing conditions to which zebra respond.

5.2.1. Feeding behaviour.

Although zebra are essentially grazing animals they do occasionally browse selected shrubs (Brynard and Pienaar, 1960; Ebedes, 1972; Fitzsimons, 1920; Van der Schijff, 1959). Gwynne and Bell (1968), who did stomach contents analyses on zebra in the Serengeti National Park, found that zebra used no more than 1,3 per cent dicotyledon material, and were thus virtually pure grass eaters. Lamprey (1963), working in a similar area in the Tarangire Game Reserve, did quantitative direct observations of feeding zebra and found that 7,43 per cent of their diet consisted of herbs and shrubs. In addition to their occasional browsing habits, zebra in the Kruger Park have been seen to dig up corms and rhizomes, particularly during dry periods (Pienaar, 1963).

Due to more important assignments a quantitative study could not be undertaken in the Kruger Park. As a substitute, the species and portions of the plant fed on by zebra were noted by direct observation whenever possible. Observations made by the local biological staff were augmented by more than 30 new species and the revised list for the Kruger Park is provided in Table 5.1. The growth-forms recorded

in this..../- 76 -

in this list represent the actual type of plant on which the animal was seen to feed.

Although the list provides no data on actual species preference, it clearly indicates that zebra have a very wide feeding spectrum.

Table 5.1.

Revised list of the plant species, specific growth form and portion of the plant fed on by zebra in the Kruger National Park.

Legend: I = inflorescence; L = leaves; Sh = sheath; St = stem.

Name of Plant	Portion eaten	Growth form
Aristida congesta subsp.congesta	I, L, Sh and St.	grass
Aristida congesta subsp. barbicollis	I, L, Sh and St	grass
Aristida graciliflora	L	grass
Bothriochloa insculpta	I, L, Sh and St	grass
Brachiaria nigropedata	I, L, Sh and St	grass
Brachiaria xantholeuca	I, L, Sh and St	grass
Cenchrus ciliaris	L and St	grass
Chloris virgata	L	grass
Cynodon dactylon	L	grass
Cymbopogon excavatus	L	grass
Digitaria smutsii	I and L	grass
Digitaria eriantha	I, L, Sh and St	grass
Digitaria pentzii	L	grass
Digitaria zeyheri	L	grass
Digitaria longiflora	L	grass
Dinebra retroflexa	I, L, Sh and St	grass
Diplachne fusca	L	grass
Andropogon amplectens	L	grass
Enneapogon scoparius	I, L, Sh and St	grass

Enneapogon..../- 77 -

Name of Plant	Portion eaten	Growth form
Enneapogon cenchroides	I, L, Sh and St	grass
Eragrostis trichophora	I	grass
Eragrostis barbinodis	I, L, Sh and St	grass
Eragrostis chloromelas	I, L, Sh and St	grass
Eragrostis superba	I	grass
Eragrostis racemosa	L after burning	grass
Eragrostis rigidior	L	grass
Elyonurus argenteus	L after burning	grass
Fingerhuthia africana	L	grass
Heteropogon contortus	I, L, Sh and St	grass
Hyperthelia dissoluta	L & St after burning also I of young plants	grass
Ischaemum brachyantherum	I, L, Sh and St	grass
Loudetia simplex	L and St	grass
Panicum maximum	I, L, Sh and St	grass
Panicum coloratum	I, L, Sh and St	grass
Pogonarthria squarrosa	L	grass
Rhynchelytrum repens	L	grass
Setaria woodii	L	grass
Setaria flabellata	I and L	grass
Schmidtia pappophoroides	I, L and St	grass
Sporobolus consimilis	I, L and St	grass
Sporobolus fimbriatus	I, L, Sh and St	grass
Sporobolus pectinatus	I, L, Sh and St	grass
Sporobolus nitens	I, L, Sh and St	grass
Sporobolus smutsii	I, L, Sh and St	grass
Themeda triandra	I, L, Sh and St	grass
Tricholaena monachne	L	grass
Tragus berteronianus	I, L, Sh and St	grass
Urochloa mosambicensis	I, L, Sh and St	grass
Urochloa bolbodes	I, L, Sh and St	grass
Urochloa rhodesiensis	I, and L	grass
Cyperus spp.	I, L and St	Sedge

Amaranthus..../- 78 -

Name of Plant	Portion eaten	Growth form
Amaranthus thunbergii	L, St and flowers	Herb
Cleome diandra	L, St and flowers	Herb
Sesbania bispinosa	L and shoots	Herb
Trachyandra saltii	L and seeds	Herb
Tribulis terrestris	L, St and flowers	Herb
Trianthema salsoloides	L, St and flowers	Herb
Zornia capensis	L and shoots	Herb
Zornia tetraphyla	L and shoots	Herb
Colophospermum mopane	Scorched and burnt leaves and twigs	Shrub
Combretum imberbe	L and twigs	Shrub
Dichrostachys cinerea subsp. cinerea	Pods	Tree
Dichrostachys cinerea subsp. nyassana	Pods	Tree
Grewia bicolor	Green twigs	Shrub
Lonchocarpus capassa	Green leaves and leaves scorched by a recent fire	Shrub
Maerua parvifolia	Leaves and twigs	Shrub
Pterocarpus rotundifolius	Scorched and burnt leaves and twigs	Shrub
Salvadora angustifolia var. australis	Green leaves	Shrub
Schotia capitata	Leaves	Shrub
Schotia transvaalensis	Leaves and twigs	Shrub
Sclerocarya caffra	Fruit	Tree

5.2.1.1. Method of feeding and associated activities.

As is the case with the various breeds of domestic horses (*Equus caballus*), the zebra has a sensitive, strong and mobile upper lip which it uses to push herbage between the incisor teeth, which then cut the grass. Loose herbage is collected with the lips and further

manipulated..../- 79 -

manipulated with the tongue. The mobility of the lips make zebra successful feeders at vegetational strata between ground level and the height of the individual's head (Fig. 5.3. and Fig. 5.4. respectively). The pattern of behaviour while grazing differs according to the condition of the pasture and the number of competing animals present. Generally, however, a group will graze in a fairly limited area. When optimal grazing conditions bring large numbers of zebra together, intraspecific tolerance is high with hundreds of animals grazing quite harmoniously a few metres apart (Fig. 5.5.).

In contrast to domestic horses (Hafez, Williams and Wierbowski, 1962; Taylor, 1954) zebra defaecate anywhere on their range and do not select areas for defaecating and areas for grazing. It is, however, interesting to note that the captive wild zebra at Skukuza only defaecated on the perimeter of their enclosure. Here it was noted that when any particular zebra developed an urge to defaecate, it would actively move from the centre of the boma to the periphery or to another established dung heap. To prove that this was not merely fortuitous the boma was cleaned out at intervals and the areas of the dung heaps mapped (Fig. 5.6.). In each case the new dung heaps were started in the same position as before. Except for the dung heaps around the two fodder holders, the others were not in places commonly used by zebra while resting. In his paper on "Grazing Behaviour and Helminthic Diseases", Taylor (1954) discusses the value of this type of behaviour to the domestic horse as a means of avoiding and reducing the ingestion of nematode and other larvae. One wonders, however, how this hygienic instinct originated in the Equidae where the ancestors were never confined to small areas of any sort. It is even difficult to explain this

Fig. 5.3. Zebra are very fond of short grasses and are capable of cropping grasses almost to ground level. West of Skukuza, September, 1971.

Fig. 5.4. Zebra browsing a Lonchocarpus capassa shrub. Just north of Lindanda, December, 1970.

Fig. 5.5. Part of a herd of over 400 zebra grazing on the Lindanda plains, February, 1969.

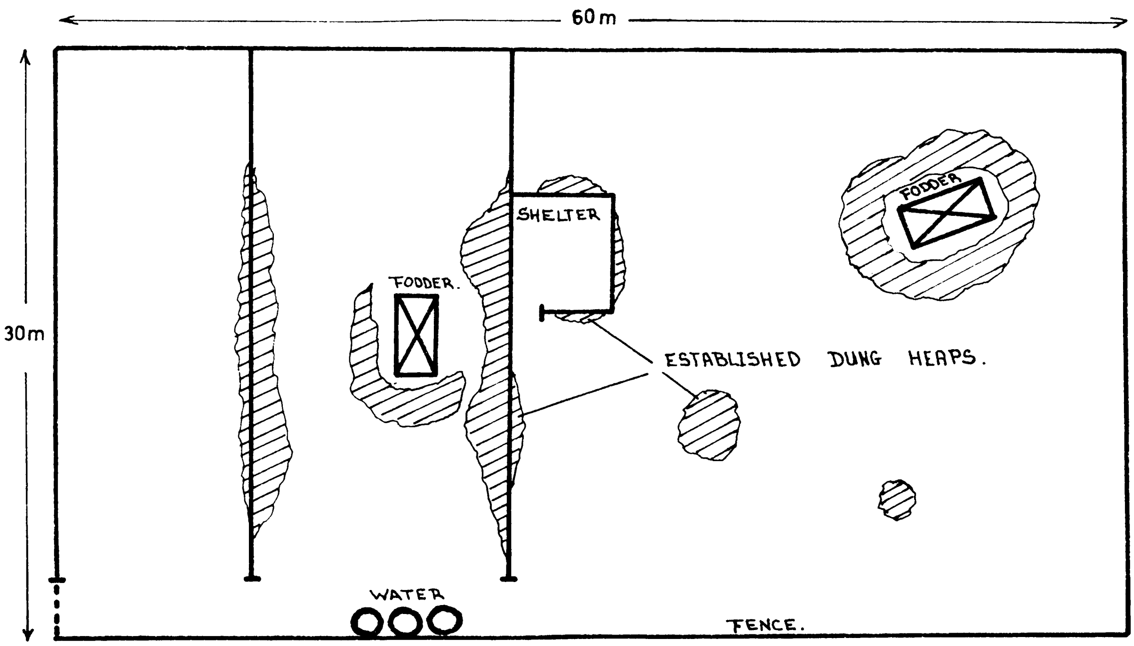


Fig. 5.6 Bomas at Skukuza showing the concentration areas where zebra actively defaecated. Intervening areas were almost unused.

type of behaviour on the basis that primitive horses developed an abhorrence to the smell of faeces of their own sort, since zebras of both sexes actively smell faeces (Klingel, 1967; and personal observations) and frequently take pieces between their lips. Additionally, young foals eat a fair amount of faeces.

Foals in the Kruger National Park estimated to be less than one week old, have been seen to smell and eat the fresh warm faeces of either their mother or another zebra. In one case a young foal was seen to ingest at least 1½ faecal segments. After feeding on the faeces it started to drink from its mother. This behaviour, which is common in domestic horses, has also been observed by Wackernagel (1965) in captive zebra at Basle Zoo. Grass feeding in foals appears to be initiated within the first few days of life. In captive animals at Skukuza it was seen to commence at five days of age. During the first two weeks grass feeding is, however, limited, the animal merely plucking or picking up odd bits of grass, chewing them slightly and then swallowing. Stomach content analyses of foals about one week old have shown that the ingested herbage is very poorly masticated, and that it makes up a small volume of the stomach contents, the rest being milk. In addition to their sporadic grazing activities young foals often pick up and chew pieces of wood or bark. Occasionally small amounts of soil may also be picked up and swallowed.

5.2.1.2. Selection of plant species and growth stages.

Observations in the field have indicated that zebra will feed on almost any grass species, provided it is short and in a young growing stage. As the grass matures, species as well as particular portions of

the plant..../- 81 -

the plant may be selected. In East Africa Stewart and Stewart (1970) found that *Themeda triandra* and *Cynodon dactylon* were consistently selected irrespective of whether these species were abundant in the pasture or not. By similar methods of faecal analysis Casebeer and Koss (1970) found a preference for *Themeda triandra* over *Pennisetum mazianum* and *Digitaria macroblephara*.

With regard to the various growth stages it is abundantly clear that zebra, as well as most plains game, are very fond of young growing grass especially when it is short or transitional (Petrides, 1956; Watson and Kerfoot, 1964). In the Kruger Park the sporadic movements of large herds of zebra and wildebeest onto areas where grass growth has been stimulated is evidence for this, while in the Serengeti-Mara Plains Region animals are known to move onto areas wet by a storm even before the grass has sprouted (Talbot and Talbot, 1963). The growth flush on burnt areas is particularly acceptable to zebra and animals will come from miles around to utilize the protein source (Fig. 5.7.). The urge to feed on fresh green grass is oftentimes so strong that captive wild zebra, normally quite unapproachable, can be coaxed to take grass from one's hand.

Although zebra prefer short or transitional grasses they do occasionally enter and feed in areas of long grass. In the Pretoriuskop area odd groups are often compelled, due to the lack of other more favourable habitat types to do this. When feeding in these areas zebra seldom take more than a few mouthfulls from a particular tuft before moving to the next and seldom graze lower than 10 to 15 cms. In contrast to wildebeest they are also less selective with respect to the portion of the grass plant taken and their diet consequently consists

of portions..../- 82 -

Fig. 5.7. Zebra feeding on the short grass (mainly *Bothriochloa insculpta*) stimulated after a fire (post burn growth flush) Guweni area, March, 1969.

of portions of both leaves and stalks. In many areas zebra only utilize long grass while in transit, i.e. either when moving between waterholes and grazing areas or when migrating. In the Serengeti National Park (Watson & Kerfoot, 1964) the major plains game (wildebeest and zebra) only graze the long grassland for a short time at the end of the wet season as they move westward to the dispersal areas, and again for a short time at the start of the rains, as they move eastward. Of these two species the wildebeest shows the most marked avoidance of the long grass zone, and they pass through it in less than one week, while zebra may remain in it for up to three weeks.

When comparing the present numbers of zebra and wildebeest in the Pretoriuskop section (1069 and 442 respectively) it is quite clear that the zebra are better adapted to the local conditions.

5.2.1.3. Other unusual feeding activities.

Although the browsing and herb feeding activities of zebra can often be correlated with locally poor grazing conditions, another factor, namely their preference for certain plants, also plays a role. On numerous occasions it has been witnessed how zebra selectively browse recently burnt or scorched Colophospermum mopane and Pterocarpus rotundifolius shrubs (Fig. 5.8.). The leaves (if present), as well as the thinner branches, appear to be relished by them and one can only presume that the sweet roasted flavour of the plant stimulates the observed behaviour. In addition to this, zebra are particularly fond of the burnt and scorched remains of grasses - before the new growth appears, and have frequently been seen grazing amongst smouldering vegetation. In these areas they avoid the unburnt patches and feed

almost..../- 83 -

Fig. 5.8. Scorched Colophospermum mopane shrubs selectively browsed by zebra and showing the extent to which the thinner branches are eaten. Nwarihlangari windmill, July, 1969.

almost exclusively on the burnt grass stubble. Stomach content analyses of these animals show that ash and scorched stubble are not unintentionally picked up, but actively selected. In Rhodesia, Johnstone (pers. comm.) shot zebra with pitch black stomach contents due to the ingestion of large amounts of ash.

Another interesting observation with regard to the feeding behaviour of zebra is the fact that in certain areas such as the Lindanda plains of the central district, they feed on the herb *Tribulus terrestris*. This weed is characteristic of overgrazed or trampled areas and is well known for its toxic effects on sheep. In sheep the plant has a photosensitizing effect on the lighter parts of the animal's skin, the results being local swelling, cracking of the skin and eventual refusal by the animal to eat (Humphrey, 1962). When grazing is sparse on the Lindanda plains during the wet season, zebra often feed on this plant and it is interesting to note that no toxic effects have been observed.

5.2.1.4. Conclusions.

It is quite clear from the previous discussion that the zebra is a grazing species which, due to its catholic taste, occasionally browses and feeds on herbs. With respect to its grazing habits it may be regarded as a highly flexible species capable of adapting to local conditions.

Although competition among the major grass feeders in the Park (buffalo, zebra, wildebeest, impala) is at present unimportant, there are indications that zebra and wildebeest are competing for food in certain parts of the central district. Both species prefer open

areas with..../- 84 -

areas with short grass and it is here that overgrazing and subsequent competition occur. In comparison to East Africa with its vast open grasslands, the Kruger Park has few comparable areas, and the zebra, being more adaptable with respect to its choice of habitat, is consequently more successful than the wildebeest.

Considering the potential competitive grazers together it is clear that, where food preferences overlap, competition is reduced due to differences in choice of habitat or due to food preference being complementary.

Similar observations have been made in East Africa (Grzimek and Grzimek, 1960a; Lamprey, 1963; Talbot and Talbot, 1962 and 1963a; Vesey-Fitzgerald , 1965).

5.2.2. Grazing conditions.

There are a number of factors which either directly or indirectly produce the grazing conditions to which zebra respond. Among these, precipitation, fire, grazing pressure and grazing succession can be regarded as being the most important.

5.2.2.1. Precipitation and fire.

Few factors have a greater impact on the movements of zebra than precipitation. To a large extent it determines the kind of plant community that will dominate a region and also produces the seasonal and permanent drinking places essential to the species. In addition to these factors the amount and distribution of precipitation affect chemical composition of plants both directly and indirectly. The direct effect is leaching of nutrients from the herbage (Laycock and Price, 1970), while the indirect effect is caused by variations in the amount of soil moisture available for plant growth.

In many..../- 85 -

In many instances it is difficult to separate the influences of fire and precipitation since both have the same general effect of stimulating grass growth. Rainfall, however, has the greater effect, since it can stimulate rejuvenation and cause sustained growth of both burnt and over- or well-grazed grasses.

Throughout the world the reaction of game to fresh growing vegetation is well known. Biswell (1969), for example, describes how by the use of controlled burning in North America, game ranges can be improved. Here the effect of fire may either be used to bring about sprouting and new seedlings, both of high palatability and nutritional value, or, to clear away dense vegetation unacceptable to certain herbivores. In Africa the movements of the larger mobile herbivores can frequently be correlated with the growth stage and hence palatability of the vegetation. The migrations of elephants from the Kibale Forest Reserve and Queen Elizabeth National Park has been correlated with the growth activity of the forage (Wing and Buss, 1970). Here, during the December-February dry season when most plant species were found to undergo some degree of dormancy, the elephants moved away towards the Ruwenzori Mountains or into the Congo where rain still fell and vegetation was actively growing. During the rainy season (March-May) these elephants gradually returned to the grasslands in the Park, while the Forest remained relatively empty. During the June-August dry season, when the physiological activity of most woody plants in the Forest attained its peak, the elephants entered the Forest from all sides. Similar observations have been made with respect to the seasonal movements of elephants in the Murchison Falls National Park (Buechner, Buss, Longhurst and Brooks, 1963) and in Ceylon (Mckay and

Eisenberg, 1971). In the Kruger National Park elephants have been found to be particularly reactive to localized early spring showers and the consequent growth activity of the vegetation. Large numbers soon gather in these areas and will undertake quite extensive movements to do so.

In section 5.2.1. the response of zebra to the post-burn growth flush and to fresh short grasses has been discussed. In East Africa the attraction of game, especially zebra and wildebeest, on to burnt areas has been described by Pratt (1967) and Watson and Kerfoot (1964), while Talbot and Talbot (1963a) state that fires in the Serengeti are as important as rainfall in affecting the movement of migratory plains animals and allowing them to maintain their preferred diet.

In the Pretoriuskop, Skukuza and Malelane sections the seasonal movements of zebra are largely dependent on the rotational burning program. This is particularly noticeable during the spring and autumn, just after the first burns. During late summer and early winter the majority of zebra in this region tend to avoid the long grass veld of the Pretoriuskop area and move into the shorter, more palatable grass communities to the east. As soon as the spring or autumn burns have started to sprout, zebra gradually return, the greatest majority being found on the recently burnt blocks.

To assess the relative abundance of zebra on burnt and unburnt grassland in the Pretoriuskop, Skukuza and Malelane sections, counts were undertaken during the spring of 1969 (November) and 1971 (September). The method employed was to drive all possible roads and fire-breaks, spending 50% of the time along both burnt and unburnt areas. Usually the vegetation on the one side of the road was burnt,

while that..../- 87 -

while that on the other was not. Results obtained are given in table 5.2.

Table 5.2.

Relative abundance of zebra on burnt and unburnt grassland in the southern district of the Kruger National Park.

Time of count	Total number of zebra counted	Number counted on burnt grassland	Number counted on unburnt grassland	Percentage found on burnt grassland
November, 1969	294	218	76	74,15
September, 1971	236	214	22	90,68

The fact that a mean of 81,5% of all zebra were utilizing spring burns which had already sprouted, clearly illustrates the role played by fire in affecting movements and distribution.

In contrast to the zebra which utilize the sour long grass veld of the Pretoriuskop area, those found in the sweeter communities are less, yet also strongly dependent on the burning program for their well being. All zebra will generally utilize the fresh grasses of a burn in preference to other areas.

Although movements on to burnt areas receiving rain are fairly spontaneous, a similar reaction is witnessed when showers fall in well or overutilized, unburnt areas. Between 9.10.70 and 24.10.70, for example, the well-utilized veld round Marheya windmill received about 30 mm of rain and by 27.10.70 over 400 zebra were counted in the

vicinity..../- 88 -

vicinity. Immediately before the rain only a few groups were utilizing the area. Amongst the zebra counted after the rain, were two marked individuals which had previously been seen 7 kilometres south of Satara camp. These zebra together with many others, had thus moved a distance of about 12 kilometres to utilize the young grasses stimulated by the spring shower.

5.2.2.2. Grazing pressure and grazing succession.

In any habitat that carries a natural community of herbivorous animals, grazing pressure is probably one of the most important factors regulating the composition and quality of the pasture. The trampling and cropping effect of game tends to keep herbage in an actively growing state and so, incidentally to retard maturity. These activities may also arrest the normal course of succession, or even reduce it to an earlier stage (Vesey-Fitzgerald 1960 and 1965).

Associated with grazing pressure is another ecological variable, namely grazing sequence. This is defined as the sequence of animals that utilize a pasture, usually heavy animals followed by light ones, the first arrivals preparing the pasture for use by those that follow. The outcome of a grazing succession is that the feeding habits of game tend to be complementary (Talbot and Talbot, 1962) or facilitative rather than competitive, with the result that, within limits, their numbers are positively rather than negatively interdependent (Gwynne and Bell, 1968).

In the Kruger National Park grazing pressure is an important factor in the regulation of the quality of forage, especially on summer ranges. By the time zebra reach these wet season ranges the grasses

have just..../- 89 -

have just started to sprout and they are consequently able to keep them at this more palatable growing stage by their seasonal grazing pressure. The selective utilization of this short grassland frequently results in the formation of a "grazing mosaic", portions of the pasture being neglected and becoming overgrown, while others are reduced to a short-grass sward. The term "grazing mosaic" is used to describe a similar situation as was noted by Vesey-Fitzgerald (1965) in the Rukwa Valley. This phenomenon is particularly obvious in marginal zebra habitat and wooded areas, where herds are inclined to utilize a relatively small area, to the almost total exclusion of surrounding well grassed regions. In the Letaba section, for example, zebra have been seen to initiate the grazing succession in regions where grasses of medium height grow. Here they close-crop the grasses and then gradually extend the size of the area by feeding on the perimeter. Eventually small groups of wildebeest may continue the succession. In the summer grazing areas of the migratory sub-populations large tracts of potentially good grazing are not utilized due to the height of the grasses and their apparent reduced palatability. These portions are only utilized after the grazing succession has been initiated by buffalo or when traditional short-grass ranges become overutilized.

In the winter ranges of sedentary sub-populations the effects of grazing pressure and grazing succession are less obvious than in those of migratory sub-populations. This is largely due to differences in the grass composition between the two sub-population areas. The winter ranges of sedentary sub-populations consist mainly of seral grass species of short to medium height, while those of the migratory sub-populations which have a complete growing season in which to recover, rank higher in the stage of succession and are generally grasses of medium to tall height. When the migratory game reach these winter ranges grasses are long, and, since the greatest majority of zebra arrive before the wildebeest, they normally initiate the grazing succession. During the first half of the winter the formation of a "grazing mosaic" is especially obvious, but gradually decreases as the season wears on. In parts of this range local herds of buffalo also play a role in initiating the grazing cycle.

5.3. Topography and soil types.

Although zebra are generally regarded as being plains loving species, they nevertheless frequently utilize areas that could better be described as mountainous or hilly.

Since plant communities are associated with certain soil types one would expect a similar yet indirect association between animals and the soil. In addition to these factors zebra have been found to avoid areas where soft, muddy soil conditions impede normal locomotion.

5.3.1. Topography.

In the northern and southern districts the mountainous regions, such as exist to the north-west of Punda Milia and Malelane respectively, are less well frequented by zebra, either due to their inacessibility or because of more favourable surrounding habitats. In these areas the vegetation consists of relatively open woodland with grasses of a predominantly palatable nature. The dry deciduous forest which forms isolated patches on the flat crowns of many hills in the Punda Milia

area, along..../- 91 -

area, along the south bank of the Levubu river, and on the Lebombo range between Pafuri and Malonga spring as well as north and south of the Olifants Gorge, represents a habitat more favourable to species such as elephant, kudu, nyala (Tragelaphus angasi), bushbuck (Tragelaphus scriptus) and steenbuck (Raphicerus campestris) (Pienaar, 1963).

In contrast to the mountainous regions just described certain similar areas are periodically visited by isolated groups or small herds of zebra. One such unusual area is the slopes and crown of Nwamuriwa mountain near Tshokwane (Fig. 5.9.). On numerous occasions zebra have been observed grazing on the rocky slopes of this isolated hill. Here they are found to move up the eastern slope and graze along natural terraces which carry a good grass cover. This behaviour is, however, largely confined to the spring months when the grasses are succulent and palatable. While occupying these areas they negotiate the loose rocky slopes with apparent ease. Wildebeest have never been seen to utilize similar areas.

5.3.2. Physical condition of the soil.

All along the eastern edge of the Park and in any other regions where soft, muddy or sticky soil conditions impede locomotion, zebra have been found to undertake local movements either of a very temporary or of a seasonal nature to firmer, better drained areas.

In East Africa similar observations have been made. Anderson and Talbot (1965) for example, mention that most wild animals appear to avoid heavy-textured soils when they are wet, possibly because of difficulty in walking and the "balling up" of the heavy clay on the animals' feet. These observations were, however, first noted by Talbot (1961) and Talbot and Talbot (1963b) with respect to the wildebeest in Western

Masailand...../- 92 -

Fig. 5.9. Zebra on the eastern slope near the summit of Nwamuriwa mountain, December, 1971.

Masailand. The dislike of zebra for waterlogged soils has also been noted by Vesey-Fitzgerald (1960). Birkenholz (1967) includes "firm footing" as a habitat characteristic ascribable to zebra and wildebeest during the wet season.

In the Kruger Park the soil types to the east of the sandstone reef are mainly of basaltic and rhyolitic origin (Fig. 1.1.). Other soil types do, however, also occur in localized areas. The basalts give rise to the heavy, dark, cotton (turf) soils characteristic of the Lebombo flats. These soils are very fertile but poorly drained and tend to become waterlogged during the rainy season. In contrast to this, the rhyolitic soils of the Lebombo mountains are less fertile, very shallow, and better drained. During the winter months water is a limiting factor in these mountains.

The movements of zebra between the Lebombo flats and the Lebombo hills during years of good rainfall are discussed in chapter 4, section 4.3.2.2. During these times the exodus of zebra from the flats cannot be correlated with factors such as grazing conditions, competition or predation, but there appears to be a link between this movement and the soft, sticky soil conditions. At this time of the year roads on the Lebombo flats are almost impassable to vehicles, while game, especially hoofed animals, find it difficult to move about. One merely has to observe their unnatural way of running or to walk over the same area oneself to realize how tedious locomotion actually is. These unusual conditions could quite conceivably initiate a feeling of insecurity and hence precipitate the observed exodus.

The areas to which these zebra move cannot be regarded as good zebra habitat since the grass cover is sparse, the terrain very

rocky and.../- 93 -

rocky and the bush generally thick. If one excluded the waterlogged condition of the flats as being an important factor in stimulating movements, it would be difficult to explain why game did not remain on the plains. The reason for this deduction is that large portions of the flat country are annually burnt in the spring and water is dispersed and plentiful. The zebra, however, ignore these prime conditions and still undertake the eastward movement.

During these times the territorial tsessebe and elephants are practically the only larger mammals to be seen in any appreciable numbers on the northern Lebombo flats.

The movements of the migratory eastern boundary zebra have also been described in chapter 4 and the difference between the northward and southward routes emphasized. It is interesting to note that not only does the northward (wet season) migratory route follow the well drained Lebombo hills, but these zebra also tend to remain in the eastern part of their summer range for longer periods during very wet summers.

When considering the Satara zebra and the eastern boundary sub-population it is clear that in contrast to those of the eastern part of the northern district, they are less inclined to move eastwards during very wet years. This is mainly due to topographical and vegetational differences between the two areas. The Lebombo flats of the central district are better drained than those of the northern district, while the vegetation and topography to the east, especially the north-east of the central district, also makes the habitat largely unacceptable to zebra. Due to these differences Satara zebra undertake very limited eastward movements.

In the..../- 94 -

In the Letaba area another interesting type of movement occurs. After the first good spring rains many zebra in this area vacate large parts of the low-lying Colophospermum mopane shrub savanna and Colophospermum mopane/Combretum apiculatum woodland which may become waterlogged, and move onto the slopes of surrounding hills or higher better drained areas. As soon as conditions become drier, they again return to the flat better grassed and less wooded regions.

5.3.3. Soil type.

A general relationship between soil fertility, food quality, and the abundance, size, health and vigour of wild animals has long been known (Dasmann, 1964). In addition to this the plant community of an area and the growth forms of individual species will to a large extent be determined by edaphic factors. These in turn determine whether the habitat is acceptable to a species or not.

In the Kruger Park the distribution patterns and abundance of zebra can frequently be correlated with the vegetation-type, and hence, indirectly, with edaphic factors. When analysing, for example, their numerical distribution with respect to the soil types on the west and the east of the central north-south bisecting sandstone reef, one finds that 66% of the zebra are found to the east of this reef and 34% to the west. Additionally, the area to the east (mainly basalt and rhyolite) only forms some 40% of the total area, while the western half (mainly granite and dolerite) forms about 60% of the total area (see Fig. 1.1.). It is further significant that the greatest number of zebra to the west of the sandstone reef are concentrated on the doleritic soils which appear at intervals along the length of the doleritic belt. This

narrow belt..../- 95 -

narrow belt extends from the southern district to just south of the Phugwane river in the northern district. In the Pretoriuskop and Malelane areas the seasonal movements of zebra are very strongly correlated with this belt (see chapter 4 section 4.3.2.3.). Here they are found to utilize the associated grasses mainly during the late summer and early winter when surrounding grasslands are in a less palatable condition. Zebra of the migratory western boundary sub-population again concentrate on the more nutritious and palatable grasses associated with the doleritic soils in their summer grazing area in Kingfisherspruit section (Fig. 1.1.).

The indirect association between game and soil types has similarly been noticed in East Africa. Petrides (1956) for example, has shown that game prefer plants growing on red lateritic soils to those growing on calcareous black clays. His study was carried out on grasslands near Nairobi. On the Serengeti plains where migratory game such as zebra and wildebeest are able to roam about freely during the wet season, their movements can be correlated with the growth form and palatability of the various grasses (Anderson and Talbot, 1965). Here the game tend to spend more time on the short grasslands. In these areas the grasses and herbs have a dwarfed growth-form, while further west their growth-form becomes progressively taller and more vigorous. In all these regions, however, the growth-form of individual species or the general character of the grassland whether it be short, intermediate or long grassland is determined by the soil type on which it grows.

In the Kruger National Park soils influence distribution and movements in three ways:

(i) waterlogged,..../- 96 -

(i) waterlogged, clayey soils, impede normal movements and where possible zebra move onto better drained soils,

(ii) different soils support grass associations of differing palatability and those of high palatability are selected by zebra e.g. the doleritic associations,

(iii) soil type determines the structure and composition of a plant community and some of these are unacceptable to zebra (see next section).

In addition to these, topographical aspects may render an area inaccessible to zebra.

5.4. Thicket Density.

Although zebra generally prefer open country they are less confined to this type of habitat than the wildebeest (Darling, 1960).

In certain parts of the Kruger Park zebra frequently enter fairly dense forest. They do, however, show a marked tendency to avoid areas where the visibility is less than 30 metres. Should they enter such areas, they will pass through immediately and not remain behind for extended periods.

To illustrate the role played by thicket density in affecting the distribution of zebra, the following examples are given:

(i) during the summer months zebra in the Letaba area selectively enter certain areas only. Before describing these areas it is important to mention that the dominant tree in this region, namely *Colophospermum mopane* and the subdominant *Combretum apiculatum* are both deciduous, the mopani being less predictable though generally inclined to be leafless during the winter months. During spring

these two..../- 97 -

these two species and other associated ones produce their leaves with a concommitant increase in thicket density.

Although the Colophospermum mopane shrub savanna occupies a relatively small area in this section, it is nevertheless an important zebra habitat. Here thicket density appears to be of little importance since the shrubs are only about a metre tall and additionally have fairly long inter-base distances. Visibility is over rather than between the shrubs and the animals have ample space in which to move (Fig. 5.10). As soon as the fertile soils in this habitat become less boggy, the zebra gradually return. In certain regions fire protection and edaphic factors have, however, resulted in a shrub form considerably taller than one metre. Here the grass cover is very similar to that in the previously mentioned habitat, with palatable species dominant. Contrasting, however, is the fact that zebra seldom enter these areas, and when found, are usually transient. In the taller mopani shrub savanna one does occasionally find clearings almost devoid of shrubs (Fig. 5.11.),and these are frequented by small herds or isolated groups of zebra.

In the mixed Colophospermum/Combretum woodland which covers a vast portion of the Letaba section, a different situation exists. This rather dense woodland, which is actually the major elephant habitat in the Park, has a reduced visibility during the summer months. Zebra do, however, frequent this habitat type, but always select the areas with reduced thicket density and greater visibility.

Dense forest areas that may carry a relatively good grass cover are habitually avoided by zebra e.g. the climax Colophospermum mopane forest in the northern district and riparian forests.

Zebra..../- 98 -

Fig. 5.10. Zebra grazing amongst <u>Colophospermum</u> <u>mopane</u> shrubs north of Bulweni windmill, February, 1971.

Fig. 5.11. A typical clearing in the taller *Colophospermum mopane* shrub savanna which was frequented by a small herd of zebra. Near Nhlanganini windmill, February, 1971.

Zebra observed moving through areas of dense vegetation and poor visibility appear nervous and highly cautious - frequently stopping, looking intensely ahead or galloping off at the slightest sign of danger. The utilization of overgrazed areas in preference to surrounding long grassland which is still in a palatable growing state must, to a large extent, also be correlated with an innate fear of lurking predators.

In contrast to the above, zebra have often been seen to enter woodland or forest areas where they have an unobstructed visibility (Fig. 5.12).

The fact that zebra choose a habitat with a clear and unobstructed visibility probably evolved in conjunction with their sociability and lack of protective or offensive weapons such as horns. Species such as kudu, nyala and bushbuck thrive in denser vegetation due to their less sociable habits and silent or secretive nature. Even if the zebra was predominantly a browser its sociality would immediately render it susceptible to predation in dense vegetation. Buffalo, on the other hand, are a more robust, aggressive species and with the added protection of their horns make a difficult prey for lions under any conditions.

5.5. Biological conditioning of the habitat.

The term "biological conditioning" is used by Calhoun (1952) to describe a condition brought about by the activities of sociable animals. Through diverse phenomena such as release of excreta, alteration of surrounding temperature and humidity, construction of trails and burrows and the development of habits, animals are continuously

altering..../- 99 -

Fig. 5.12. Two zebra resting in savanna woodland with tall grass. Pretoriuskop area, October, 1971.

altering their environment. These activities may in turn alter the behaviour of their own or later generations.

In zebra populations, biological conditioning similar to that observed in small mammals is frequently seen. The daily or seasonal activities of these zebra, whether they be grazing activities (grazing pressure, grazing succession, choice of certain grasslands) or the incidental construction of trails between waterholes and grazing areas or between winter and summer ranges, tend to ameliorate the habitat so that survival rate is increased. The animals consequently often exhibit a reluctance to leave the altered habitat with which they have become familiar. The home range characteristic of zebra can be linked with this last mentioned factor.

Although the concerted activity of individual zebras in a herd may intially be advantageous e.g. keeping grassland short and nutritious over a large area and thus also reducing cover for predators, it eventually becomes deleterious. The deleterious effects are due to the reduction or depletion of one or more vital requirements. On summer ranges, for example, food and water may be the eventual limiting factors and when one or both is depleted the animals must move to another area.

In conclusion one may say, that due to their concerted activities, zebra condition their habitat to the extent that it becomes more habitable and, consequently, a reluctance to leave develops. Eventually, due to a reduction or depletion of one or more vital requirements, the concerted activities become deleterious and the animals must move or migrate to another area.

5.6. Inter-..../- 100 -

5.6. Inter- and intraspecific competition.

When observing the free association between zebra and most herbivorous species, except elephant and buffalo, it becomes obvious that the physical presence and behaviour of other herbivores have little effect on their distribution and movements. In the case of elephant and to a lesser extent buffalo, competition is limited to waterholes where drinking times may coincide. The voluminous quantities of water taken by large herds of elephant or buffalo drinking at artificial reservoirs may deplete the water supplies to the extent that zebra will have to move to a neighbouring waterhole to quench their thirst.

In certain cases interspecific competition for grazing can also result in population shifts or changes in distribution. In the Kingfisherspruit section inter- and intraspecific competition between zebra and wildebeest resulted in a gradual reduction in the number of both species which spend the summer there (see chapter 2, section 2.2.1.). At present, however, their numbers again appear to be increasing.

5.7. Predator pressure.

The continuous occupation of a waterhole by a pride of lions may cause zebra groups to move to another area, but these movements are usually temporary and have no effect on large portions of the population.

During the dry winter months prides of lion frequently hunt almost entirely around important watering points such as Mnondozi dam. The large herds of zebra and wildebeest drinking from these points are hardly affected by the lions, as the normal drinking pattern is rein-

stated soon..../- 101 -

stated soon after a kill has been made. The extended presence of lion around such watering points may, however, have a long-term effect on the game in that it could eventually lead to a breakdown of the normal reluctance to leave an area with which they have become well acquainted (see section 5.5.).

While grazing away from waterholes the presence of predators has little effect on stimulating a noteworthy movement away from the area. Should a lion be sensed but not seen, zebra will immediately evacuate the area and at times even move up to a kilometre or more away. The panic stricken activities of one group are usually sufficient to stimulate others in the vicinity to undertake the same movement. On the other hand, should zebra see a stalking lion they may initially gallop away but often some turn back to observe the movements of the predator (Fig. 5.13). In some cases they will follow a lion and approach to within 40 metres or less of it. Once the lion realizes that it has been seen, it will usually move off and zebra will continue with their normal activities - one or two always looking intently about.

When lions are resting they are ignored by zebra which do, however, remain a safe distance away.

5.8. Sociality.

The social behaviour of zebra is conspicuous in that there is a strong social attraction between the individuals of a particular family or stallion group and between the stallions of different groups (see also Klingel, 1967). In addition to this the zebra is a gregarious animal with groups frequently congregating to form large herds. The best definition of this instinctive type of behaviour is given by Allee

(1940) who..../- 102 -

Fig. 5.13. A herd of zebra approaching a lioness after she had been stalking them. At this stage the lioness had given up the stalk as she realized that she had been spotted. South of Ngotsa dam, January, 1971.

(1940) who states that "sociality is co-extensive with the existence of an innate inherited pattern of a certain specialized appetite". The satisfaction of this appetitive behaviour demands that animals live together and engage in common activities.

The fact that zebra are gregarious by nature often tends to localize their distribution in that aggregations are frequently formed in certain areas while similar ones close by are avoided. During the summer months, for example, large concentrations of migratory zebra can be found in the Lindanda/Kingfisherspruit areas (see Fig. 5.5.). Although these zebra are initially brought together by optimal grazing conditions, the aggregation is intensified due to the sociality of the species. Had they been a less social species one would have expected a more even distribution over larger portions of the summer range.

5.9. Shelter seeking.

All organisms, from the lowly paramecium to man, have one behavioural trait in common - shelter seeking. All seek optimum environmental conditions and avoid dangerous and injurious ones (Smith, 1966).

As far as zebra are concerned, there is only one form of shelter that they occasionally require and that is shade. Shelter from wind and rain or other unfavourable climatic conditions is unimportant, while shelter from predators implies the choice of an open habitat which affords the animal a clear vision and path of retreat.

Although zebra are less dependent on shade than dark skinned animals such as wildebeest and buffalo (Young, 1970) they do nevertheless utilize it, when available, during the hotter part of the day

(Fig. 5.14). ..../- 103 -

Fig. 5.14. A zebra family group resting in the shade of a large *Sclerocarya caffra* tree. Along the Metsimetsi river, January, 1971.

(Fig. 5.14). In the Kruger Park zebra are frequently seen in regions where there are no suitable shade-trees while on the Serengeti zebra range onto the open plains where there is no shade (Baldwin, 1971). Similar observations were made in the Rukwa Valley by Vesey-Fitzgerald (1960).

It thus appears that escape from the direct effects of solar radiation is relatively unimportant in the zebra's choice of habitat and that the animal posesses other means of thermoregulation. Recent experiments undertaken by Baldwin (1971) have in fact shown that not only does the black and white striping of the zebra serve as possible camouflage pattern (Cott, 1957) but that it enhances thermoregulation by optimizing radiative heat exchange. By telemetric methods, he, for example, found that the black and white stripes maintain temperature differences and that such temperature differences were capable of actual reversals under changing radiation loads i.e. when moved from shade into direct sunlight. In this experiment the temperature recorded below a white stripe rose above that recorded simultaneously below a black stripe when the animal was moved from the shade into the sun.

5.10. Wind.

The influence of wind on the movements of zebra could either be direct or indirect. Indirectly, wind velocity and direction influences precipitation due to its effect on both temperature and relative humidity (Humphrey, 1962). Excessive wind movement, by removing moisture - bearing air and replacing it with drier air, increases the evaporation potential. In semi-arid regions such as the Eastern Transvaal Lowveld periods of greater than normal wind would be a deterrent to

maximum..../- 104 -

maximum forage production - especially during the spring months. Directly, wind, by way of its ability to carry either volatile chemical substances or particles such as smoke, could entice game into a new area. The rapidity with which zebra locate and concentrate on recently burnt areas must be associated either with smell or sight or both. The same could be said of precipitation. In the case of veld fires strong winds frequently disperse smoke so rapidly and over such distances that one in fact often smells the fire before seeing it.

5.11. Temperature and humidity.

Although temperature and humidity are closely correlated it is clear that temperature has a marked individual effect on the daily activity of zebra (Young, 1970). Indirectly temperature could also affect distribution due to its effect on the rate of development, phenology and total yield of plants.

Just as temperature influences the daily activity of zebra it has been shown that humidity effects their activities and general behaviour away from waterholes (Young, 1970). The possible direct effects which temperature and humidity could have on the seasonal movements of zebra would, however, be difficult to assess, since by undertaking such movements the animals would still not be able to escape their desiccating influence.

5.12. Light (radiant-energy).

Light is of utmost importance to animals. Firstly it is essential to their food plants for photosynthesis and secondly it can affect grazing animals directly in two ways:

(a) through..../- 105 -

(a) through photosensitization after the animals have eaten certain plants (chapter 5, section 5.2.1.3.) and,

(b) by affecting breeding (Sadlier, 1969) and general behaviour (Smith, 1966).

The influence of light on general behaviour is largely confined to differences in nocturnal and diurnal activities, but seasonal migratory responses are known to uccur in certain animals. Light as a possible migratory stimulus has been discussed in chapter 4, section 4.3.1.5.

5.13. Drought.

The effects of drought are obvious in that it could affect both the water supplies and vegetation of an area to the extent that game would eventually have to vacate the region. A general drought lasting from 1961 to 1969 was, for example, one of the causal factors involved in the reduction of the numbers of zebra and wildebeest in the Kingfisherspruit area. This reduction was characterised by a partial emigration from the region.

5.14. Possible mechanisms by which zebra locate fresh grazing.

The fact that game such as zebra respond so rapidly to burns and fresh grazing leads one to believe that sensory modalities are employed in the location of these potential sources of protein, and that their arrival is not merely fortuitous. In some instances discovery of these areas could conceivably be by chance, as zebra are restless by nature. In this case, however, one would expect a slow or sporadic influx of animals onto a chosen area and not the sudden arrival of groups or herds from all directions.

In section..../- 106 -

In section 5.2.2.1. of this chapter examples were given of the movement of zebra onto burns, or onto well grazed areas that had recently received rain. While in their summer ranges, especially during drier years, zebra are particularly reactive to local showers and vast population shifts in response to proximate showers have frequently been observed in the Satara and Lindanda areas. Although these movements are only over distances of 10 to 20 kilometres they are usually of sudden onset and completed in less than 24 hours. The route followed is also direct towards the site of the rainfall. In the Serengeti Talbot and Talbot (1963) found that wildebeest and zebra moved to an area wet by a storm, often arriving before the grass had sprouted. In Botswana Birkenholz (1967) found that any change in the weather such as thunder or lightning or rain, precipitated an immediate movement in that direction. Similarly Lamprey (1964) found that zebra and wildebeest would move up to 40 kilometres in a night towards the site of rainfall and he also mentions seeing them galloping towards a rainstorm 8 kilometres away. Darling (1960) who did an ecological reconnaissance of the Mara Plains came to the conclusion that wildebeest sense newly fallen rain by olfactory means and that sight possibly also plays a role.

From these examples it thus seems fairly safe to conclude that sensory modalities are employed in the detection of fresh grazing and that vision and olfaction are the most important. In this respect zebra demonstrate true tropistic behaviour in contrast to the other alternative, namely chance discovery.

5.15...../- 107 -

5.15. Ecological separation between zebra and wildebeest.

To assess accurately the degree to which these two species are able to maintain ecological separation would require a detailed comparative study of the wildebeest's habitat requirements. Observations do, however, indicate that, although they frequently associate (Keast, 1965), this association is largely confined to drinking periods and to the times when movements between drinking sites and grazing areas occur.

During the rainy season competition is largely avoided due to the abundance of food and water. Although large herds of zebra and wildebeest may be found in the same general area, they do tend to segregate and mixed associations are usually limited to small herds and groups seeking social security. Basic ecological separation, however, lies in the different tolerance of the two species for bush and wooded country, zebra being more inclined to enter wooded areas than wildebeest. Similar observations were made by Darling (1960) and Lamprey (1963).

Chapter 6..../- 108 -

Chapter 6.

HOME RANGE

In contrast to Grévy's zebra (Equus grévyi) (Klingel, 1969), Burchell's zebra and the mountain zebra (Equus zebra) (Klingel, 1968b) are non-territorial. In the Ngorongoro Crater (Klingel 1967 and 1968a) and in the Kruger Park it has, however, been observed that zebra groups annually utilize only a small portion of the available habitat. This homing quality and the animal's attachment to the area has marked effects on their distribution and movements.

According to Jewell (1965), who restates the definition of a home range given by Burt (1943), this term may be defined as "the area over which an animal normally travels in pursuit of its routine activities".

Home range limits of individually marked zebra in the Kruger Park were ascertained by direct observation over a period of one year. Boundaries were fixed by the standard method of plotting the individual sightings on a map and then connecting the peripheral points. The area of the resulting polygon could then be calculated. Unfortunately there were insufficient sightings to compute accurate home range sizes for all the sub-populations, but an average size could be calculated for units (3), (4), (6), (7) and (8). Two home range sizes could also be calculated for unit (2) and one for unit (5). Some of these home ranges are illustrated in Fig. 6.1. The results of the calculations together with an average size for the central and southern districts and the entire Park are provided in Table 6.1.

Table 6.1...../- 109 -

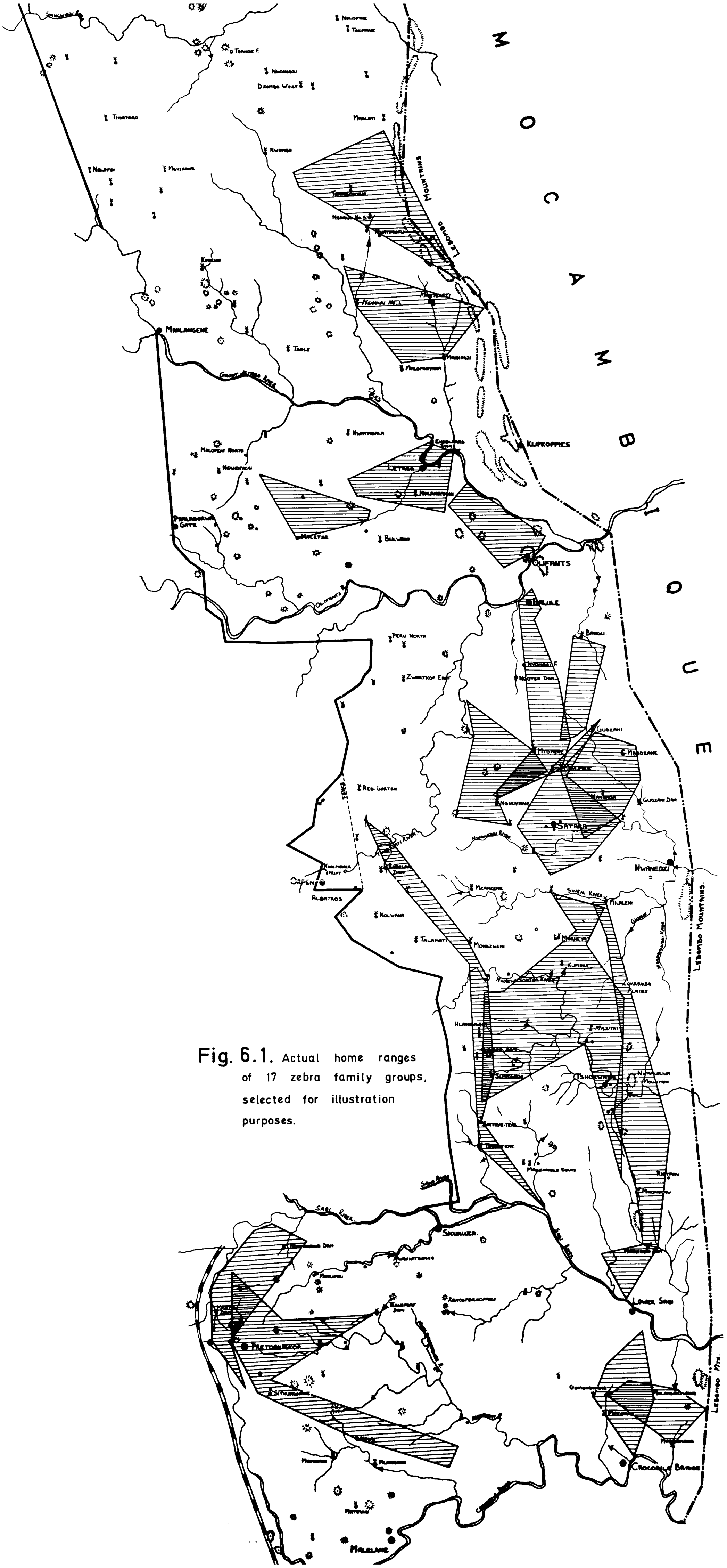


Fig. 6.1. Actual home ranges of 17 zebra family groups, selected for illustration purposes.

Table 6.1.

Mean home range sizes for the various zebra sub-populations, the central and southern districts, and the Kruger National Park as a whole.

Name of sub-population and unit number as per Fig. 4.3.	Mean size of Home Range (sq. km)	Individual Home Range sizes (sq. km)		No. of Home Ranges used to compute mean size
		Maximum	Minimum	
Shingwidzi-Letaba (Unit (2))	262	-	-	2
Letaba (Unit (3))	117	197	78	8
Satara (Unit (4))	166	566	49	23
W-boundary (Unit (5))	195	-	-	1
E-boundary (Unit (6))	193	346	97	6
Pretoriuskop-Skukuza-Malelane (Unit (7))	207	390	86	7
Crocodile Bridge (Unit (8))	111	146	69	3
Central district	171	566	49	30
Southern district	178	390	69	10
Kruger National Park	167	566	49	50

In every case the size of an individual home range reflects the area utilized by a family group, which consists of one adult stallion

plus one..../- 110 -

plus one to five mares and their foals. In no case is there a correlation between the size of the group and the size of its home range.

Although the migratory zebra of the western and eastern boundaries could be regarded as having separate winter and summer home ranges, the migratory route has been included in the computation of their home range size. This is essential since a varying period of time, depending on local conditions, may be spent in the transitional passage area. Jewell (1965) regards the migratory route as not being part of the home range.

The relative shapes and sizes of a number of selected home ranges can also be gleaned from Fig. 6.1. It must be remembered that although an individual group has a fixed home range, this area may be partially or totally overlapped by the home range of one or a number of other groups. Home ranges with a minimum of overlap unfortunately had to be selected for illustration purposes.

6.1. Factors affecting home range size in the various sub-population units.

Depending on the mobility of an animal, its energy requirements and the habitat, the size of its home range may vary from a fraction of an acre e.g. the opossum (*Didelphis marsupialis*) - 0,5 acres (Fitch, 1958) to 3840 sq. km e.g. the wolf (*Canis lupus*) in Alaska (Burkholder, 1959). Similarly one would expect differences to occur within a single species - depending on its environment.

Since home range is fundamentally an area with a certain productivity that meets the energy requirements of the individual or group that occupies it (Jewell, 1965), knowledge of measures such as the normal

density at..../- 111 -

density at which the animal lives, and biomass or standing crop, which indicate the numbers of animals a given habitat can support, should help to elucidate variations in the home range size of the particular species. In addition to these possible long-term effects, factors such as sudden climatic changes, variations in the availability of water, food, fires or predation could also affect the size of an individual home range. Another long-term factor important in regulating the size of a particular home range is the general acceptability of the habitat with respect to the particular species concerned i.e. if the habitat is optimal or marginal.

In addition to variations in home range sizes of a particular species in different habitat types, the home range of a particular individual may vary from one year to the next. In the central district, for example, where adequate observations on the movements of marked zebra were available for two-year periods, successive home range sizes varied considerably. Typical results over a two-year period for two groups were as follows:

(i) 179 sq. km (1969) and 159 sq. km 1970/71,

(ii) 203 sq. km (1969) and 142 sq. km 1970/71.

In addition to these differences it was found that a particular group was not necessarily dependent on a specific home range, but that it could, in fact, utilize two quite separate portions of the sub-population's range during succeeding years, or that parts of the home ranges could overlap.

Zebra, being a tremendously mobile and restless species, it is obvious that should home range size be computed over a period of five or more years, it could quite conceivably eventually cover most,

if not all..../- 112 -

if not all of the range of the sub-population. Klingel (1967), for example, illustrates the home ranges of four groups in the Ngorongoro Crater for the period 1963 to 1965. During this time one of these groups utilized an area of about 147 sq. km, while the total area of the crater (Goddard, 1967) is only some 260 sq. km.

6.1.1. Density and Biomass.

Provided a given area had a high primary productivity, one would similarly expect a high density of species suited to the particular habitat. Biomass figures would be affected in the same way.

Since an animal's movements are largely determined by its energy requirements, primary productivity would be relevant to an interpretation of its home range size. Biomass and density on the other hand, although dependent on the productivity of the area, could affect a particular animal's home range size in quite a different way. This indirect effect could be in the form of increased social interactions resulting in an intolerance and consequently more extensive patterns of daily and seasonal movements, or even an emigration from the area.

When surveying the densities of zebra in the various sub-population units and comparing this to corresponding home range sizes it is quite clear that this factor is unimportant. In fact one merely has to look at zebra density in the three districts to see that its effects are not at present operating. In the central district, for example, (Table 4.1.) there is one zebra per 45 hectare, while the mean home range size is 171 sq. km. In the southern district, on the other hand, there is one zebra per 138 hectare, while the mean home range size is 178 sq. km., i.e., although density is much lower than

in the central..../- 113 -

in the central district, the home range size is greater. These differences obviously reflect reactions to the habitat and not to density. Comparing the density of zebra in the Kruger National Park (one zebra per 94 hectare) with that of the Ngorongoro Crater (one zebra per 5,2 hectare) (5038 zebra in 260 sq. km) (Turner and Watson, 1964) it becomes overwhelmingly obvious that, at this stage, home range size in the Kruger Park is independent of zebra density. The same conclusion can be made when comparing home range size with the density of large and medium sized herbivores (Table 6.2.).

Table 6.2.

Densities of large and medium sized herbivores in the three districts of the Kruger National Park

District	Number of large and medium sized herbivores	Number of hectare per animal
North	58933	16,9
Central	126050	4,4
South	60747	5,8

Biomass can similarly be proved to be unimportant and by alluding to figures calculated by Pienaar (1966b) the following deductions can be made:

(i) although the Crocodile Bridge sub-population has the smallest home range (111 sq. km), it has a high density of zebra and the second highest biomass of competing herbivorous species in the whole Park,

(ii) in the Letaba sub-population, with the second smallest

mean home..../- 114 -

mean home range size, a similar set of conditions exists. Here, however, the greatest numbers of zebra are found towards the east where habitat conditions are more suitable. The area does, however, have a high biomass of herbivores due to the large numbers of buffalo and elephant,

(iii) in the Pretoriuskop-Malelane-Skukuza area, with the largest home range size, the actual area utilized by zebra supports a very low biomass of herbivores.

Comparing the herbivore biomass for the whole of the Kruger National Park (10529 lbs per sq. mile) (Pienaar, 1966d) with that of the Ngorongoro Crater (35000 lbs per sq. mile)(Lamprey, 1964), where zebra groups have much smaller home ranges than in Kruger, it again becomes clear that this factor is unimportant.

Considering the development of a density-dependent inter- or intra-specific intolerance due to high herbivore densities and its possible effect on the zebra's home range size and general movements, it is clear that this factor is at present of no significance. Burchell's zebra, in fact, is an animal which, due to its gregarious instinct and sociality, lives harmoniously at relatively high densities. This type of behaviour contrasts markedly with that of territorial antelopes, or species such as the roan antelope, where each inhabits a certain area (activity zone) (Joubert, 1970) to the almost total exclusion of other herds. In these species, social behaviour has a marked effect on species density, home range size and general movements.

6.1.2. Characteristics of the habitat.

Having discussed the various factors that affect the zebra's choice of habitat, distribution, movements and migration in chapter 5,

it should..../- 115 -

it should be clear that any of these factors could potentially also affect both the shape and size of an individual group's home range. To determine which factors are operating with respect to a particular sub-population unit would require the analysis of the movements of each individual group, and then a generalization for the area as a whole. This would be a laborious and relatively unimportant task, since most of the deductions have already been made in chapter 5.

The most obvious effects of habitat on home range size can, however, be demonstrated by comparing two extremes, namely the small home range of the Crocodile Bridge sub-population (111 sq. km) with that of the Pretoriuskop-Malelane-Skukuza sub-population (207 sq. km).

In the Crocodile Bridge area the large numbers of zebra have a good supply and distribution of water at their disposal. In addition, the excellent, well grassed parkland aspect of large parts of the habitat makes it an optimal area for zebra. The fact that these zebra are rather confined with respect to their movements (smallest sub-population unit of the eight) cannot be an important restriction, since none of the marked groups moved over the entire available habitat during the course of a year. In the Pretoriuskop-Malelane-Skukuza unit, on the other hand, zebra also have a good supply and distribution of watering points at their disposal, but the difference lies in the habitat. This area, large portions of which are covered with fairly dense woodland and tall unpalatable grasses, must at present be regarded as one of the poorest zebra habitats in the whole of the Kruger Park. Potentially the area, however, has a high carrying capacity with respect to zebra and prior to 1947 it used to harbour large herds of zebra and wildebeest (see chapter 2, section 2.3.2.). Due to the sub-optimal habitat conditions these zebra have to range over wider areas in search of the conditions which they prefer. Not only does the condition of the habitat affect the movements of these zebra, but it also has profound effects on the social structure of individual family and stallion groups. These aspects will, however, form part of a later publication.

One may thus conclude that the large home range size for the various sub-populations (between 111 and 262 sq. km) or for the Kruger National Park as a whole (167 sq. km), can largely be ascribed to the low carrying capacity of the range (when compared to an area such as the Ngorongoro Crater) and to large portions being sub-optimal habitat, either seasonally or annually, with respect to the zebra.

6.2. Significance of home range.

When observing the sightings of individual marked zebra groups within their home range, it becomes clear that certain areas form foci of activity, while others are less frequently visited. The foci of activity are the waterholes which are visited almost daily, the animals then moving away either to graze or rest. Each home range thus consists of an area where the animal can feed, drink, rest and reproduce. Depending on its immediate need the animal can, at any time, move to any part of its home range. The ease and accuracy with which zebra, which have travelled many kilometres, locate a waterhole leaves one with no doubt that they are well acquainted with all the features of the terrain within their home range. Here they are familiar with the paths best suited for their use, the best waterholes or grazing areas, the best refuges and with situations where danger usually lurks. In addition to this, the home range habit stablilizes the community organization by reducing the amount of turmoil that would result if all the animals were constantly moving about (Dice, 1952).

Chapter 7..../- 117 -

Chapter 7.

AGE DETERMINATION

For any large mammal study, whether it be on social behaviour, reproduction or population dynamics, it is essential to have a method of ageing the study animal. Frequently in the past, and even today, studies have been undertaken on species for which accurate ageing criteria are not available. Although many of these studies are justified, it often leads to unnecessary duplication of work and waste of research effort. With the techniques and research staff available today more emphasis should be placed on ageing criteria and in many cases techniques developed years ago should be revised and improved, where necessary. The need for this type of data is acute, especially in areas where game is confined to fenced reserves and their numbers are artificially manipulated. To calculate reliable culling quotas one has to have at one's disposal such age specific data as the potential mean age at first parturition, age at which birth of last offspring occurs, mean life expectancy and data for inclusion into life tables, population age structure curves and mortality curves. The importance of this type of data is stressed by Fairall (1969), Hewer (1964), Simpson (1966), Taber (1960), Quick (1960) and many others.

At present research is also being carried out on the reproduction and population dynamics of zebra in the Kruger Park and it has thus been deemed necessary to check whether the tooth development and wear stages derived by Klingel and Klingel (1966) for the plains zebra (*Equus burchelli boehmi*), also apply to *Equus burchelli antiquorum*. Because these two sub-species live under slightly different ecological

conditions..../- 118 -

conditions one would expect differences to occur especially with regard to the degree of incisor wear. On the other hand these differences may be so slight as to be of no consequence.

Although the excellent pioneer work done by Klingel & Klingel (1966) served in many ways as a guide, the methods used here, both in recording the changes in the table surfaces of the incisors, measuring the annual incisor wear and the ageing criteria, are quite different.

7.1. Materials and Methods.

7.1.1. Animals used in the study.

(i) Late term foeti collected from culled mares destroyed in the culling program.

(ii) Eight foals between birth and two months of age were destroyed in the field. Additional foals between three and six months of age were abundantly supplied by the culling program.

(iii) Between 1969 and 1971 the skulls of over 700 culled zebra were collected and stored at Skukuza. These represented animals from about one month of age to old age. All the sub-adults and adults were shot randomly with respect to sex and age, as after about two years of age it is impossible to estimate a zebra's age from its external appearance.

(iv) Ten zebra between 1½ and 3½ years of age were captured in the central district and marked as previously described. The number in each respective age class and their ages at the time of marking was as follows:- Three of 1½ years; one of 1¾ years; one of 2 years; one of 2½ years; two of 3 years; one of 3¼ years and one of 3½ years. The oldest animal in this group was thus 4½ years old when eventually destroyed.

(v) Forty-two..../- 119 -

(v) Forty-two adult zebra between four and 14 years of age were captured and marked. Seventeen of the 42 were marked in the southern district and had to be omitted from the age determination study due to a shortage of time and a difficulty in relocating them.
The 25 remaining animals (20 ♀♀ : 5 ♂♂) were marked in the central district.

(vi) Seven of the captive zebra described in Table 2.1. were also utilized. According to Erz (1964) and Klingel and Klingel (1966), there are no differences in tooth development between stallions and mares, except for the canines. This, together with the fact that adult stallions were more likely to lose their collars, resulted in more mares being marked.

7.1.2. The eye lens technique.

Since the introduction of eye lens weight as an indicator of age in the cottontail rabbit (Sylvilagus floridanus) by Lord (1959), the technique has become increasingly popular and has been used on numerous mammal species. Although more valuable for use on small and medium-sized mammals (Child, Sowls and Richardson 1965), it has been applied with success to certain large mammals. Laws (1967), for example, used it on the African elephant to indicate the precision of other ageing criteria (replacement and wear of the mandibular dentition), while Fairall (1969) used it to derive the age structure and life table of an impala population.

In the case of zebra the main objective was to determine whether the procedure had any practical application with respect to ageing individuals and to see whether it could be used as a test for the other ageing techniques applied.

Both eyeballs..../- 120 -

Both eyeballs were excised from 102 zebra (30 ♀♀ and 72 ♂♂) from the central district of the Park and treated as follows:

(i) Injected with 10% formalin and fixed in formalin for one to two weeks,

(ii) Lenses were removed, cleaned, and then dried to a constant weight in a ventilated oven at 100°C. This took between four and eight weeks depending on the size of the lens. In some cases lenses took up to three months to reach a constant weight.

(iii) After removal from the oven the lenses were cooled in a desiccator (over silica gel) and weighed.

All zebra were aged by the standard technique described later in this chapter, the mean weight calculated for each lens pair and the age/lens weight curve (Fig. 7.0) plotted for the two sexes together.

7.1.3. Annular structure of tooth cementum as an index of age.

In contrast to zebra in East Africa (Klingel and Klingel, 1966), zebra in the Kruger Park show fairly clear annual rings in the cementum of permanent incisors (Fig. 7.10 and 7.11) and molars. For convenience only I_1 from the upper jaw was used when determining the number of rings, since this tooth is easier to work with and the rings are much clearer.

Basically the method consisted of cutting the tooth longitudinally, selecting the area with the thickest cementum and then grinding the portion down to a suitable thickness on an electric grindstone. This sample was then further ground down by hand on very fine abrasive water-paper. The thickness of a section was decided by trial and error so that just sufficient light could pass through it for

observation..../- 121 -

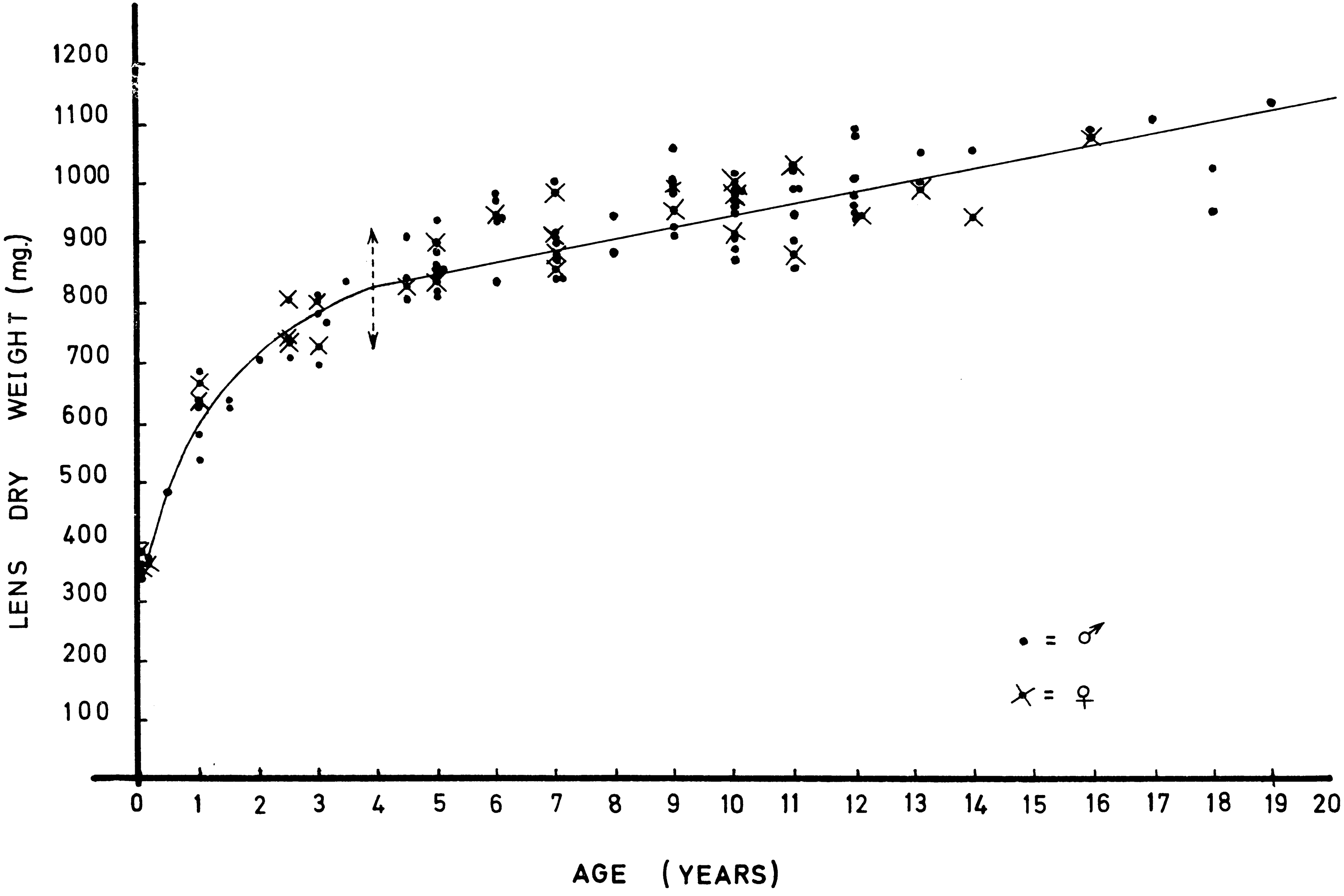


Fig. 7.0. Growth curve for eye lenses. (n=102 pairs).

observation under a compound microscope. Generally the best results were obtained when the section was examined under water. Sections could, however, also be examined after mounting (D.P.X.) although the optical differentiation between layers did decrease in certain instances (see also Hewer, 1964). In contrast to the work of Low and Cowan (1963), Spinage (1967) and Simpson and Elder (1969), no staining technique was employed and decalcification was unnecessary.

Because the root of I_1 continues to grow until the animal is about seven years of age, a region had to be selected where growth had ceased at a fairly early age and where cementum had been laid down. The most appropriate region was found to be the lingual curve of the incisor, just above the subterminal root boss (Fig. 7.4. No. 4(R)). Since the first layer of cementum is laid down in this region when the animal is about $2\frac{1}{2}$ years old, a correction factor of $2\frac{1}{2}$ had to be added to the number of cementum layers counted. For animals up to two years of age cementum rings could be counted on the labial surface of I_1 in the middle region of the tooth.

7.1.4. Ageing criteria.

Since one frequently requires the ages of both live or freshly killed zebra as well as those of old skulls, ageing criteria have been separated, where possible, into these two categories. This type of grouping is, however, only possible until the animal is four years old, as after this age all the permanent premolars, molars and incisors are in wear.

Criteria used for assessing age are: eruption of the deciduous (milk or temporary) incisors, both through the pre-maxillary

bone and..../- 122 -

bone and the gum, and their degree of wear; replacement of the milk incisors by the permanent incisors; degree of wear of the permanent incisors; size and shape of the infundibula and the shape of the table surface of these teeth; eruption of the canines in stallions; eruption of the deciduous premolars and molars through the maxillary bone and the gum and their stages of wear; replacement of the deciduous premolars by the permanent premolars and their stages of wear.

In most cases the eruption and replacement of opposing incisors and premolars and the eruption of the molars take place more or less simultaneously and the description refers to both upper and lower jaw. Wear of the incisors, however, refers only to the upper jaw.

7.1.5. Description of the growth and morphology of zebra teeth.

As in the case of the domestic horse, and in fact all the recent Equidae (Klingel and Klingel, 1966), the dental formula of *Equus burchelli antiquorum* is as follows:

Milk dentition: $\frac{\mathrm{Id3\ Cd1\ Pd4}}{\mathrm{Id3\ Cd1\ Pd4}}$

Permanent dentition: $\frac{\mathrm{I3\ C1\ Pd1\ P3\ M3}}{\mathrm{I3\ C1\ Pd1\ P3\ M3}}$

(I = incisor, C = canine, P = premolar, M = molar, d = deciduous tooth).

The in situ arrangement of the incisors, premolars and molars is given in Fig. 7.1. With regard to the canines, only adult stallions have these fully developed and they can be used with safety to determine the sex of the animal (Fig. 7.2.). Permanent canines in stallions, however, only erupt through the gum at between $3\frac{1}{4}$ and $3\frac{1}{2}$

years of..../- 123 -

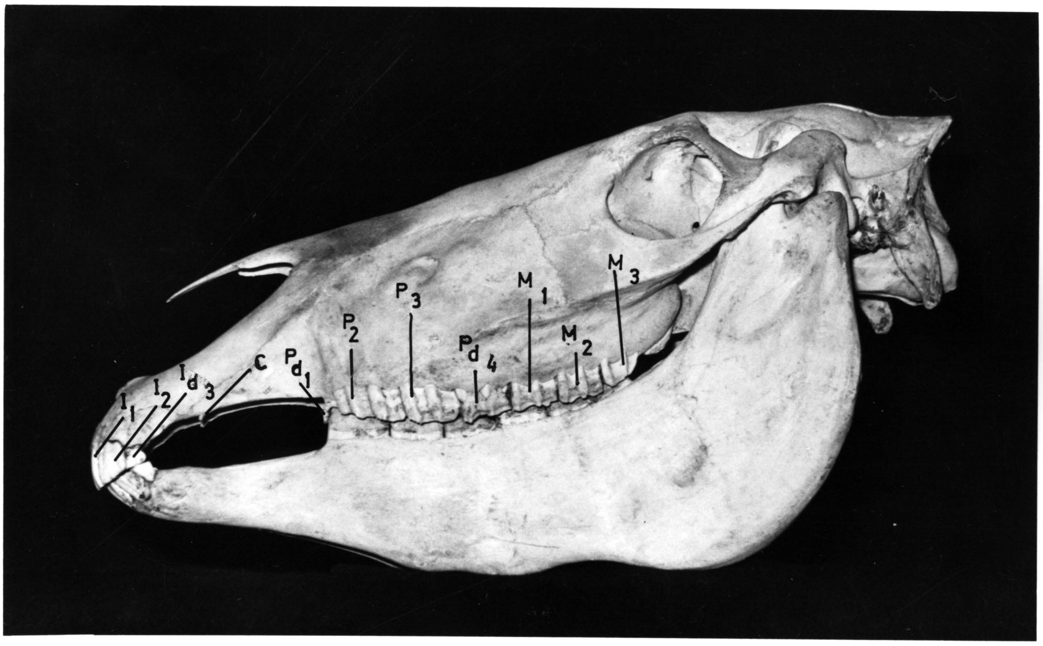


Fig. 7.1. Arrangement of teeth in a $3\frac{1}{4}$ year old zebra mare. Note that Pd_4 is almost worn away and forms a "cap" on top of P_4 which is just visible below it. M_3 is not yet fully in wear. The tiny canine is typical of adult mares.

Fig. 7.2. An example of sexual dimorphism in the canines of an adult stallion (left) and an adult mare (right). The mare actually has unusually large canines, being one of the largest specimens found.

years of age. Rudimentary permanent canines are frequently found in mares, but are much smaller than the permanent canines of stallions, have quite a different shape (Fig. 7.2. and 7.1.) and often do not pierce the gum. Milk or deciduous canines are present in young animals of both sexes, but never pierce the gum. Milk premolars (Pd_1) are of no consequence in assessing age since both eruption and wear varies considerably from animal to animal and they may remain in position to an advanced age or fall out before the animal is three years old.

The milk incisors differ from permanent incisors in that the former possesses a definite neck (Fig. 7.3.). In addition the milk incisors are rounded where they meet the gum, with a small triangle of gum between each tooth and the next. Permanent incisors run parallel to each other and are more square cut, with little or no gum between them. Moreover, the deciduous incisors have a smoother texture and are whiter and smaller than the permanent incisors. It is normally very easy to distinguish permanent from temporary incisors, especially when both are present in the mouth. Inexperienced workers could, however, confuse temporaries and permanents in yearlings and five to six year olds. In these two age classes the shape and size of the infundibula are not sufficiently different to distinguish between the two. (See Fig. 7.23, carbon prints 8, 9 and 16).

Possibly one of the most interesting aspects of the zebra's dentition is the infundibulum found in all incisors. This is a characteristic peculiar to the Equidae (Miller and Robertson, 1959) and consists of a dark depression or hollow running down the centre of the incisor for a variable length. (Fig. 7.4.). From the table surface of the incisor there is an infolding of the enamel resulting in the

formation of..../- 124 -

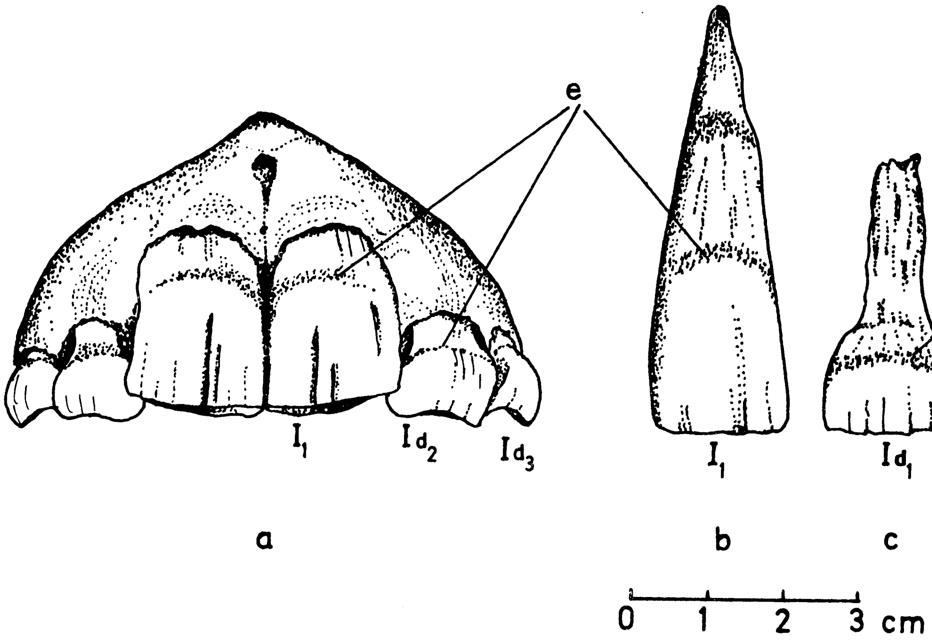


Fig. 7.3. Differentiation between upper permanent and temporary incisors.

(a) Anterior view of premaxilla.
(b) Labial view of I_1.
(c) Labial view of Id_1.
(d) Lateral view of Id_1 just before it is replaced by I_1. Note how the root has been partly resorbed and the amount of wear on the crown.
(e) Gum line.

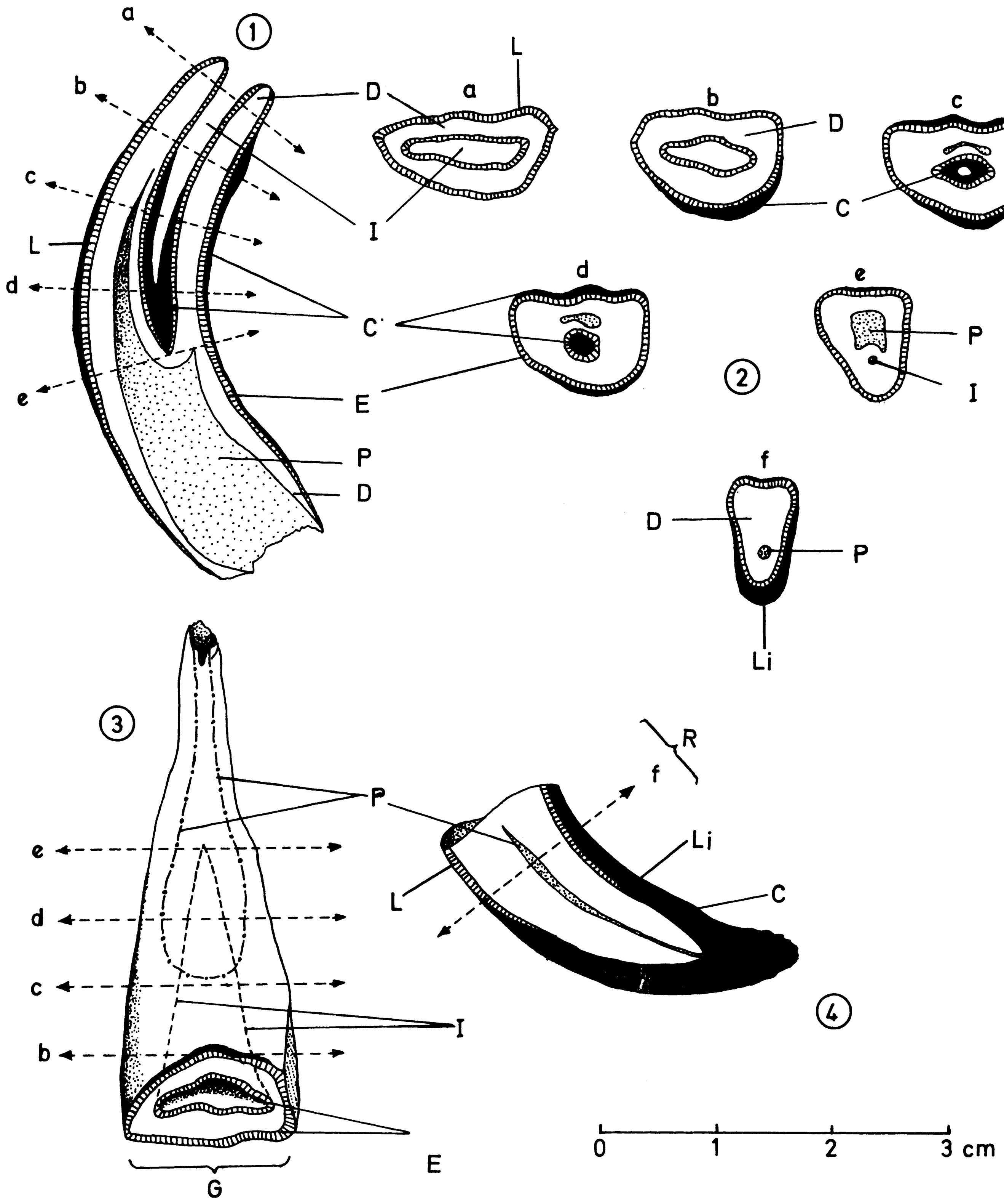


Fig. 7.4. Morphology of the first upper incisor (I_1). (1) Sagittal section of I_1 just before it starts wearing. Depending on the animal a varying amount of cement may be laid down inside the infundibulum. (2) Cross sections through I_1 to show the changing shape of the table surface and infundibulum at various ages. (a) 3 years (b) 6 years (c) 9 years (d) 12 years (e) 14 years (f) 18 years. (3) Lingual view of I_1 at 6 years showing the funnel shape of the infundibulum, the large pulp cavity and open root. (4) Sagittal section of I_1 (16 years) showing the closed root, the pulp cavity almost filled with dentine and the thick layer of cement on the root.

Legend: C=cement, D=dentine, E=enamel, G=table or grinding surface, I=infundibulum, L=labial surface, Li=lingual surface, P=pulp cavity, R=region from which sections were taken to count cementum annuli.

formation of a hollow tapering funnel which eventually closes at its proximal end as the tooth continues its development. The longest infundibula are found in I_1, where the mean length is 31.03 mm. (Table 7.1.).

To determine the length of the infundibula the first and second permanent incisors of 10 different animals were sectioned longitudinally using an electric band saw. The section was made from the table surface to the root of the incisor.

By sectioning incisors before they had erupted it was also possible to determine when the infundibula of I_1 and I_2 had completed their development. This was found to be at approximately one year for I_1 and two to $2\frac{1}{2}$ years for I_2. Since I_1 and I_2 start wearing at three and $3\frac{1}{2}$ years respectively, teeth extracted from the appropriate animals in which the infundibulum had completed growth yet where the tooth had not yet, or just started to wear, could be used to determine the infundibular lengths. (See Table 7.1.) The reasons for determining infundibular development and length in I_1 and I_2 is explained in a later section of this chapter.

The development and growth of incisors is initiated from their distal end and long before the tooth has ceased to grow, the table surface and crown have completed their growth, i.e. this portion of the tooth is similar to that of the same tooth when it eventually erupts. In I_1 the crown completes its development at between 10 months and one year (erupts at $2\frac{1}{2}$ years), while in I_2 the crown has completed its development at one to $1\frac{1}{2}$ years (erupts at $3\frac{1}{4}$ years). In both these teeth further growth is represented by a general thickening of the various layers and a proximal increase in length.

Just before..../- 125 -

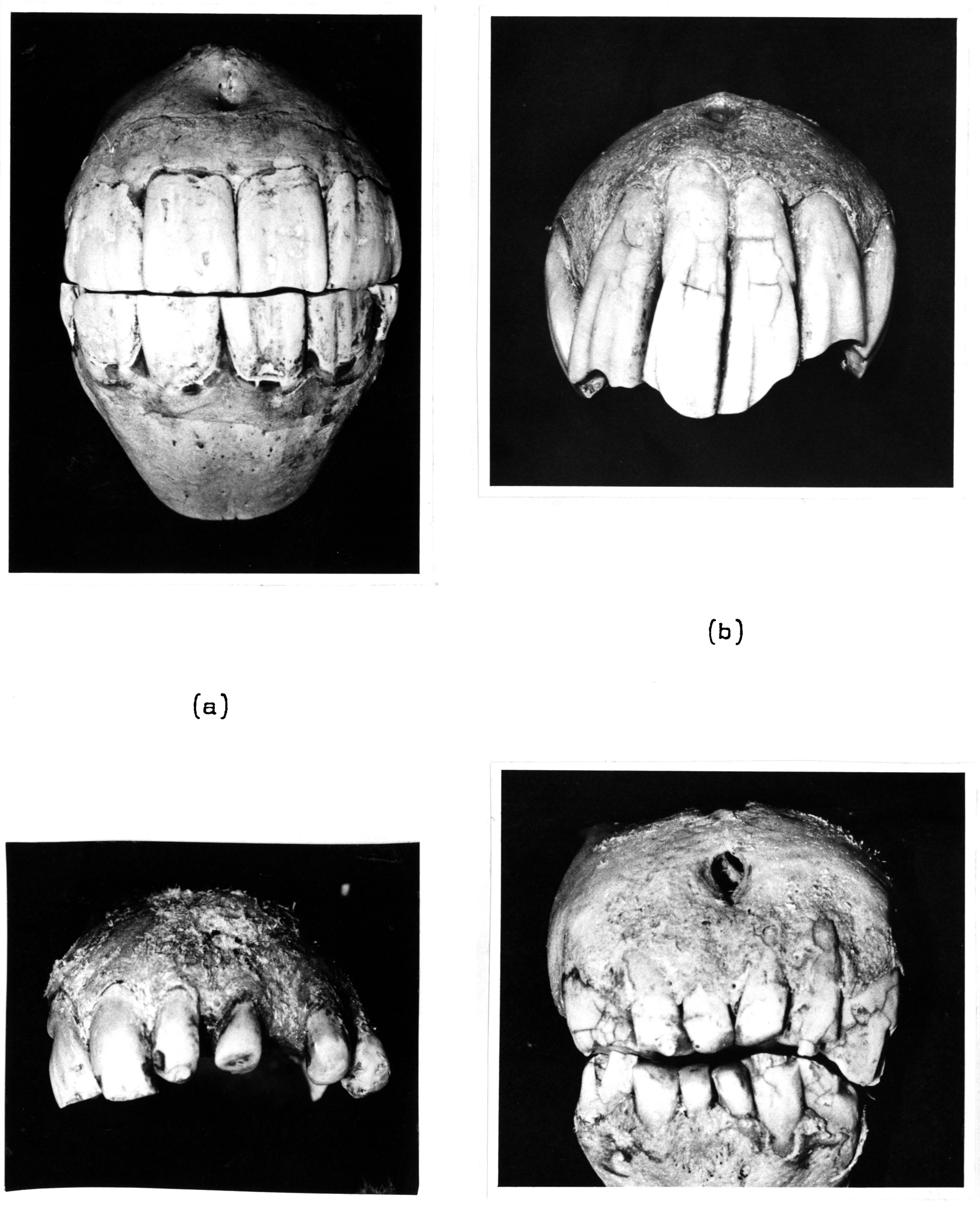
Just before the incisors start wearing they reach their maximum length, their roots penetrating deep into the bone of the premaxilla or mandible. After about 3½ years of age, further growth of I_1 and I_2 is represented by the addition of cementum to their outer surface and base. The tooth thus still continues to grow in length but is at the same time being worn down by the feeding process. At five to seven years of age growth at the base slows down as the pulp cavity is filled with dentine and slowly closed off. After this age the tooth is actually pushed forward and upwards in the alveolus by the formation of spongy bone at its base, little tooth growth taking place. By the time the animal reaches old age the alveolus is about ¼ the depth of that of a 4½ year old animal. In animals with an uneven bit the wear of a particular permanent incisor may exceed the natural growth and in these cases the incisor is soon worn down level with the mucous membrane of the gum (Fig. 7.5.).

Table 7.1.

Mean infundibular lengths for I_1 and I_2 measured on teeth in which the infundibulum had completed its growth, yet where the tooth had not yet started to wear.

I_1		I_2	
Age of Animal (years)	Length of Infundibulum (mm)	Age of Animal (years)	Length of Infundibulum (mm)
1½	34,05	2	28,00
2	36,80	2½	26,20
2	26,95	2½	27,00
2½	29,80	3	27,50

Table 7.1. cont...../- 126 -



(b)

(a)

(c)

(d)

Fig. 7.5. Comparison between a normal bit (a), an unevenly worn bit (b) and the bits of two very old animals (c) and (d). In (b) and (c) only the upper jaws are shown. Specimen (a) is 3¼ years old, (b) is 7–9 years old and (c) and (d) 18–20 years old.

Table 7.1. cont.

I_1		I_2	
Age of Animal (years)	Length of Infundibulum (mm)	Age of Animal (years)	Length of Infundibulum (mm)
2½	28,55	3	28,50
2½	28,45	3	26,10
3	26,50	3½	27,25
3	34,75	3½	27,00
3	32,20	3½	30,02
3	32,25	3½	29,50
Mean length =	31,03 mm	Mean length =	27,71 mm

As the permanent incisors grow in length in their bony alveoli, the deciduous incisors are being worn away. When the table surface of the permanent incisor reaches the root of the deciduous incisor, the lingual portion of last mentioned is gradually absorbed (Fig. 7.3.) the permanent incisor thus moving in below the deciduous incisor. The final result is that the permanent incisors erupt in exactly the same position as their deciduous predecessors.

Due to the formation of the infundibulum in the incisors and its lining of enamel, a partially worn tooth shows two enamel rings on the table surface (Fig. 7.4.). These enamel rings present sharp edges which facilitate the cropping of grass (Young, 1950). In the permanent incisors the shape of both the outer and infundibular enamel rings have been used as ageing criteria. Because of the relatively constant tapering shape of the infundibula of the permanent incisors and the gradual wear of each, a continuously changing pattern is pro-

duced on the..../- 127 -

duced on the table surface of the tooth. A stage is eventually reached when the infundibular enamel ring disappears, since the level of wear has passed below the depth of the infundibulum. Additional to the disappearance of the infundibulum, the outer shape of the tooth changes from an oval to a triangle, and eventually to a quandrilateral, since the tooth is tapered from crown to root. (Fig. 7.4.).

The molars (cheek teeth) of which there are six or seven present in each quarter of the jaws (depending on whether Pd_1, the wolf tooth, is present or not) are typical of the Perissodactyls, being lophodont and hypsodont. The first three permanent molars are represented in the milk dentition and are therefore sometimes called premolars. The roots of permanent premolars and the molars are long and there is but little tapering from the crown downwards - an arrangement allowing maximum wear (Miller and Robertson, 1959).

7.1.6. Methods employed in determining the various age classes.

Before any age classes were decided upon, the order of tooth eruption, replacement and wear was determined by arranging all skulls into a series from the youngest to very oldest. The results obtained here were similar to those described by Erz (1964), Klingel (1965), Klingel & Klingel (1966) and are also very similar to those found in the domestic horse (Miller & Robertson, 1959). A combination of information obtained from captive and free roaming zebra was then used to derive the various age classes ((1) to (27)).

For age class (1) the teeth of late term foeti were examined both fresh and after being cleaned of all soft tissue. Newly born foals were either shot or reared in captivity where their teeth could be observed periodically.

Age classes..../- 128 -

Age classes (2) to (8). Data on the tooth development of these age classes were obtained mainly from captive animals. One skull of known age was obtained from the roan antelope (*Hippotragus equinus equinus*) enclosure at Nwashitsumbe. This animal was nine months old. Captive foals and immatures were either immobilized periodically, or when tame enough, their incisors were examined during feeding sessions. By relating the stage of eruption of these incisors to the incisors of zebra destroyed in the field, it was possible to determine the corresponding pattern of premolar and molar eruption.

Age classes (8) to (15). These classes were determined from immature and sub-adult zebra marked in the field. These animals were recaptured after six and 12 months or recaptured after six months and destroyed after 12 months. Additional data on molar replacement and wear was obtained as described under age classes (2) to (8) above. In four of these zebra, data on the wear of the permanent incisors was also collected as described under the next group of age classes. In all cased carbon prints were made of the table surfaces of the incisors (Fig. 7.6. and 7.7.).

Age classes (16) to (27) (Adults). These animals were either recaptured or destroyed after 12 or 18 months. Captive animals were not used to determine these age classes.

Since all adult animals are aged according to the shape of the infundibula and table surface of the incisors and since these criteria are directly dependent on the amount of incisor wear, two methods were developed to gauge this wear.

(a) Instead of making use of photography, direct contact carbon prints were made of the table surface of the upper incisors of each

immobilized..../- 129 -

Fig. 7.6. Making a carbon print from the incisors of a 13 year old mare after she has been marked.

Fig. 7.7. After applying pressure through the paper onto the table surface of the incisors the carbon paper can be removed and the resultant contanct print filed.

immobilized specimen. This method is based on the fact that the enamel ring around the incisor and/or infundibulum projects slightly above the general table surface of the tooth - due to being harder than the surrounding dentine. For this procedure 10 cm x 10 cm squares of ordinary office carbon paper were fixed onto pieces of foolscap paper of the same size, using cellotape at the two opposing ends. The carbon surface was placed so as to face the paper. By laying the outer surface of the carbon paper against the table surface of the six incisors and pressing down with one's thumbs or fore-fingers a perfect print of the table surface of each incisor is produced. (Fig. 7.6. and 7.7.). From these carbon prints the exact shapes and dimensions of each infundibulum could be obtained and these could be compared with ones obtained from the same animal a year or two later. The advantages above photographic prints include:

(i) quicker and less work involved,
(ii) direct comparisons can be made with prints made at a later date as they are true reproductions of the table surfaces,
(iii) measurements can be taken from the carbon prints and give exactly the same results as those taken from the tooth itself,
(iv) the prints are small and handy to file,
(v) the method is very cheap.

These carbon prints are currently being used to keep a record of all zebra skulls collected.

(b) In addition to the carbon prints annual incisor wear was measured directly on 20 marked zebra by the following technique:

Using a..../- 130 -

Using a carpenters hand drill fitted with a $^3/64"$ diameter steel bit, a tiny hole was drilled through the enamel on the labial surface of three or four incisors, about eight to 12 millimeters away from the grinding surface (Fig. 7.8.). The distance from this hole to the junction of the labial and table surfaces of the incisor was then measured using a vernier calliper (Mitutoyo-Japan) graduated in $^1/20$ths of a millimeter (Fig. 7.9.). When these animals were subsequently recaptured or destroyed the distance was remeasured and annual wear calculated.

The animals for which data on annual incisor wear were available were then arranged into five age groups, representing zebra from 2½ years to 14 years of age (Table 7.2.) and the mean annual incisor wear for each incisor for the animals in each group was calculated. Animals were separated into the five age groups by utilizing the following information:

(i) the number of growth (annual) rings in the cementum of I_1. These incremental rings or lines could be determined for animals between two years and old age, and corresponded well with known age animals (Fig. 7.10 & 7.11),

(ii) accurate ages were obtained from field observations of animals from 2½ to five years of age. In these animals the measurement of incisor wear was not essential for the determination of age,

(iii) carbon prints obtained from marked zebra (5 years old to old age) recaptured or destroyed after one or two years, facilitated the allotment of an animal to a specific age group. This could be done by estimating

the animal's..../- 131 -

Fig. 7.8. Drilling the reference hole through the enamel on the labial surface of I_2.

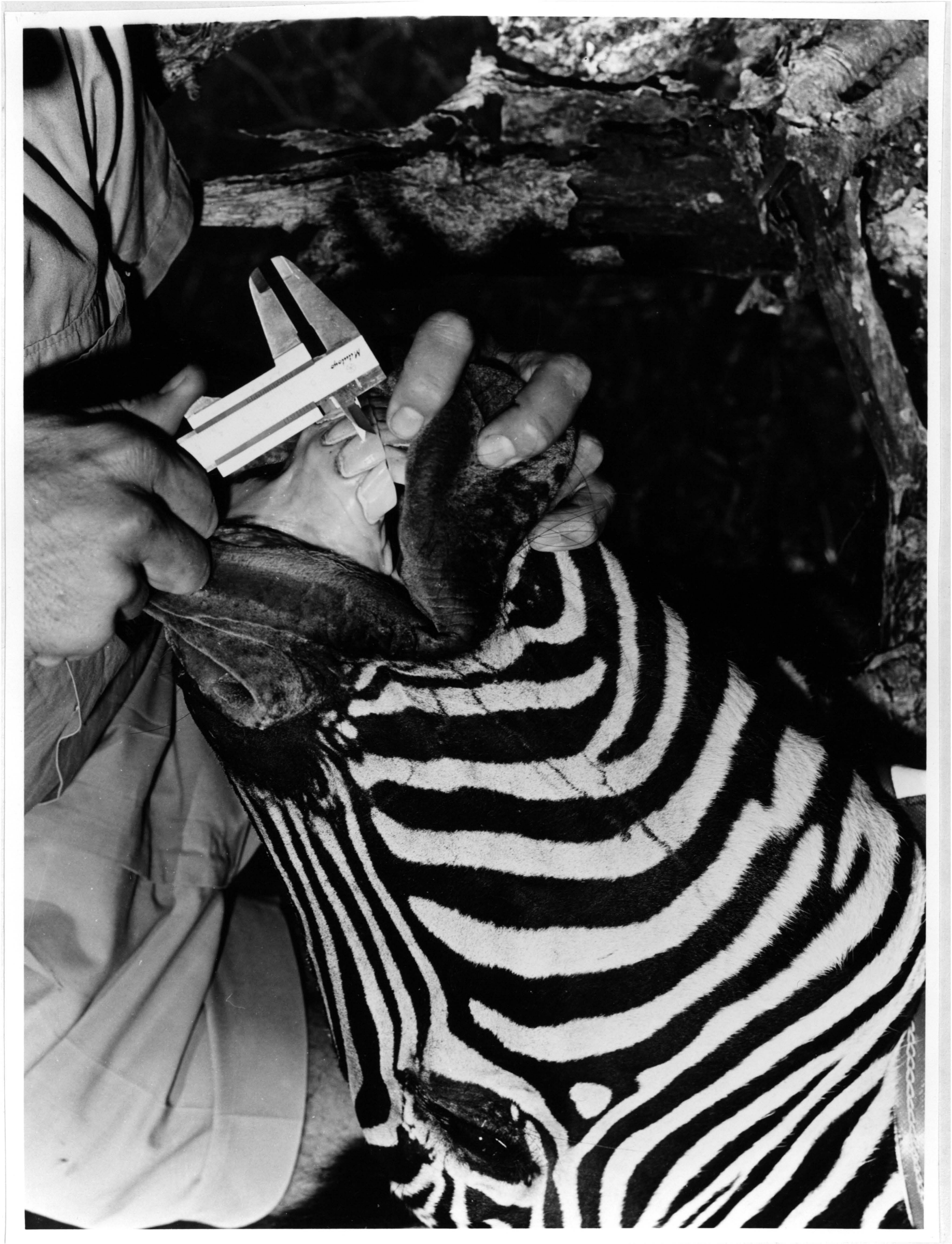


Fig. 7.9. Measuring the distance from the reference hole to the junction of the labial and table sufaces of the specific incisor.

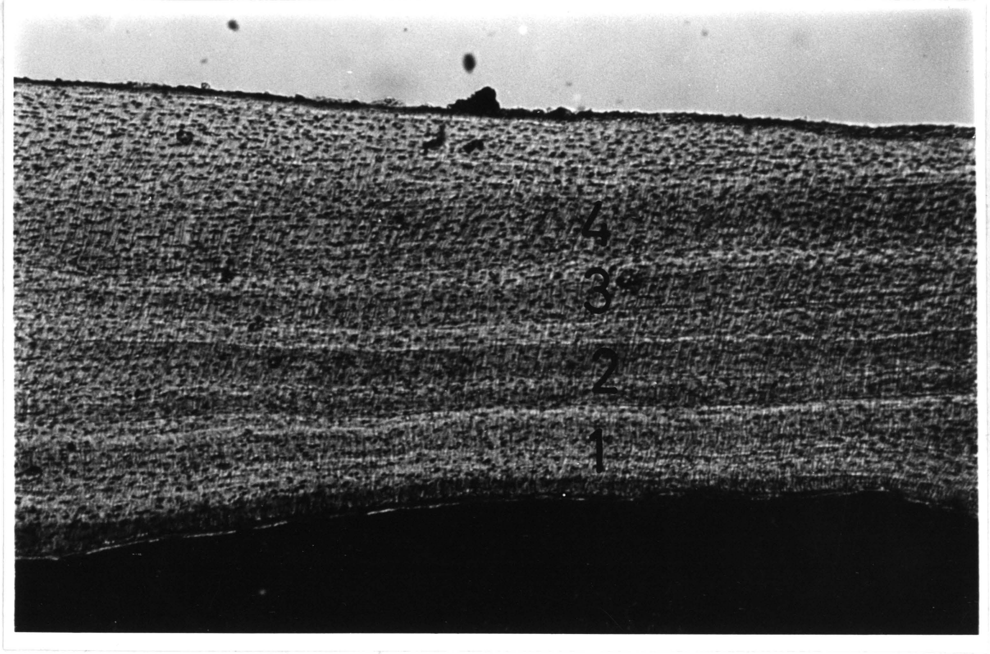


Fig. 7.10. Longitudinal section of the cementum of I_1 from a 7 year old stallion. The fifth annual ring is incompletely laid down. ($4\frac{1}{2} + 2\frac{1}{2} = 7$ years) (x 50).

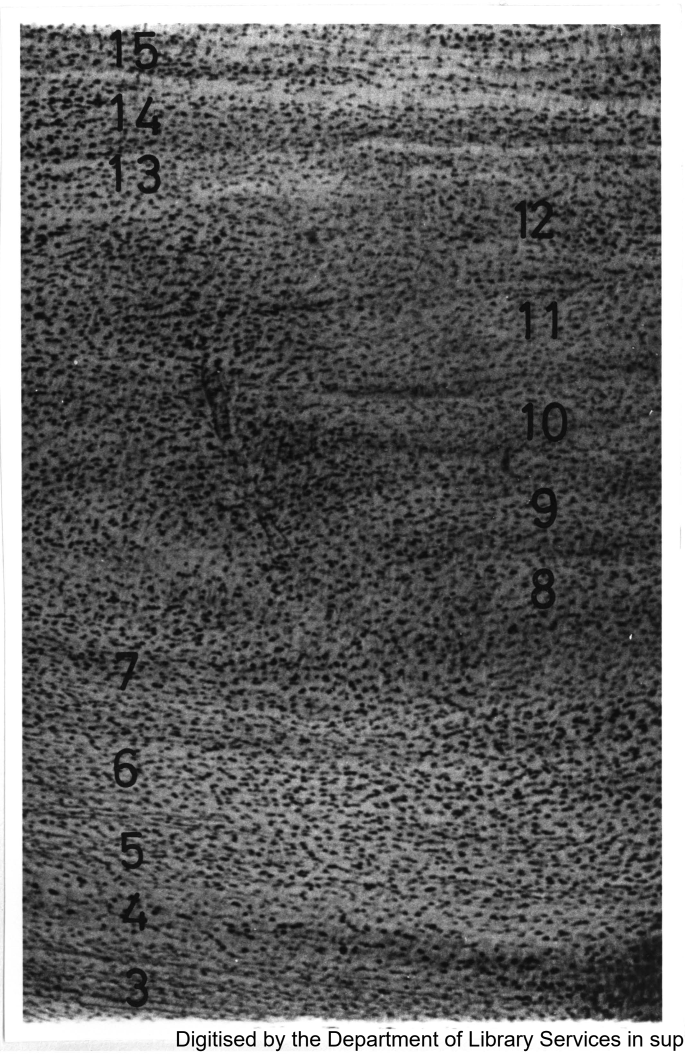


Fig. 7.11. Longitudinal section of a portion of the cementum of I_1 from a $18\frac{1}{2}$ year old mare. In obscure cases such as this, counting was facilitated by switching. The longer the section the easier the count (x 50).

> the animal's age at first capture (using five year olds for comparison), and then again after the interval of one or two years.

Annual incisor wear for I_1 and I_2 of each age group was then plotted against the age group (Fig. 7.12.) and the resultant curve extrapolated to cover the old age classes for which data on incisor wear were not available.

Using the annual wear for each individual incisor and for zebra of specific ages as indicated by the abovementioned graphs, it was thus possible to add, for example, three or four successive years incisor wear together and to cut this amount of tooth away using an electric band saw. Starting with the youngest animals (4½ years old) and doing three or four complete sets of incisors for each age group, it was thus possible to reproduce artificially the picture of incisor wear as it occurs in the field. Teeth cut down from 4½ years to eight years would then help in the selection of a naturally worn eight year old bit. This bit could then in turn be cut down by three years wear to give the eleven year old bit. To do this, annual incisor wear from eight to nine, nine to ten and ten to eleven years was obtained from the graph, added together and cut away from the appropriate incisor. The artificially obtained 11 years old template was then again used to select a naturally occurring 11 year old bit (from the 700 skulls available) and the procedure repeated.

Table 7.2...../- 132 -

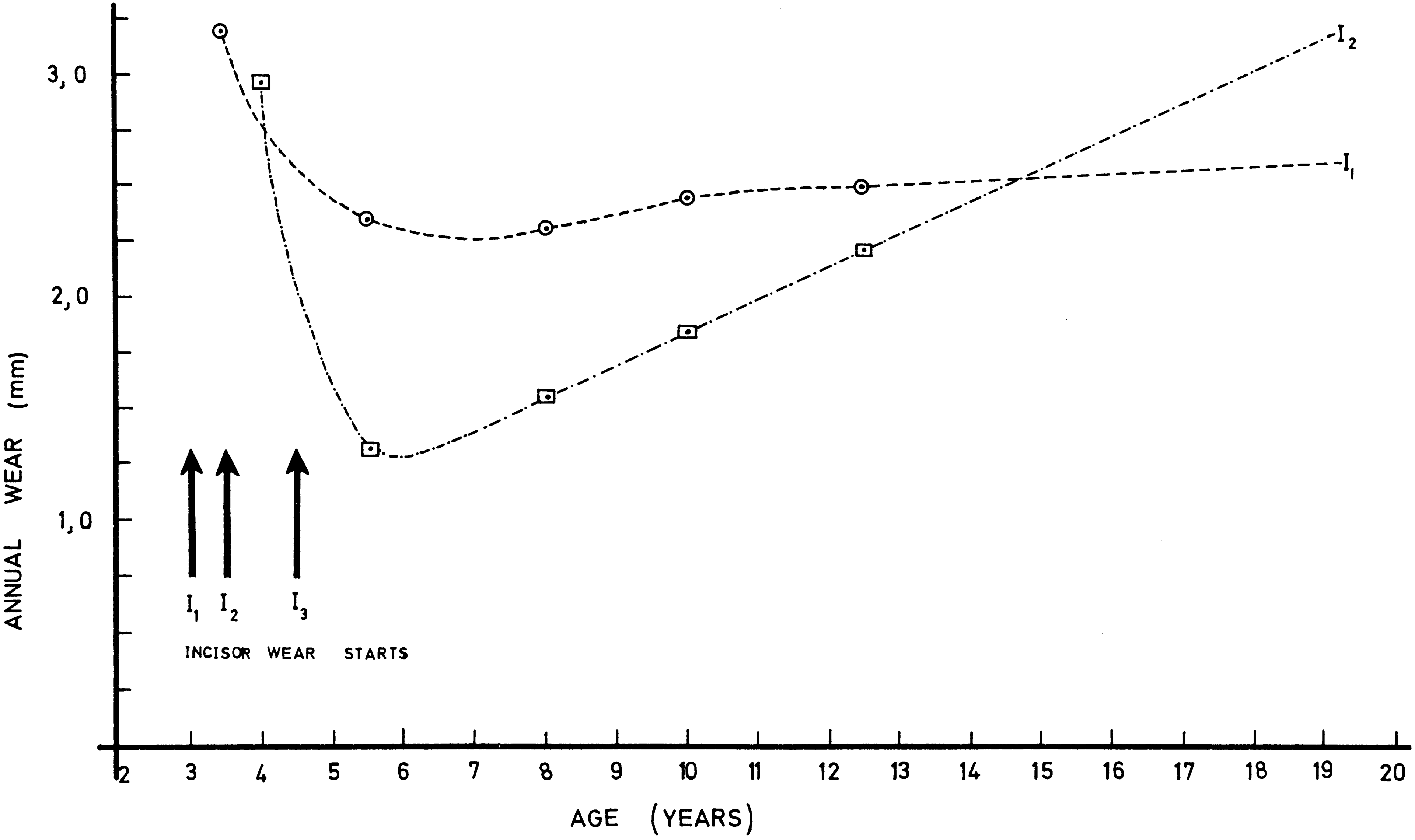


Fig. 7.12. Curves illustrating varying rate of wear of I_1 and I_2 with age.

Table 7.2.

Table illustrating the mean annual incisor wear (I_1, I_2 and I_3) for zebra divided into five different age groups (1 to 5)

1. Age group $2\frac{1}{2}$ to 4 years

No. of animal	No. of days between marking and recapture	Age when marked (years)	Annual wear (mm)		
			I_1	I_2	I_3
W 1	175	$2\frac{1}{2}$	2,66	-	-
R □	195	$2\frac{1}{2}$	3,89	-	-
R 13	345	$3\frac{1}{4}$	3,44	-	-
R 3	214	$3\frac{1}{2}$	2,82	2,98	-
Mean annual incisor wear =			3,20	2,98	-

2. Age group 5 to 6 years

B 1	526	6	1,84	0,59	-
W 5	161	5	3,63	1,99	-
R 5	398	6	2,00	1,61	-
W 3	443	5	2,46	-	-
R G	348	6	1,65	1,05	1,10
Mean annual incisor wear =			2,32	1,31	1,10

3. Age group 7 to 9 years

R E	380	7	2,21	1,35	-
W 15	177	9	2,37	1,75	1,03
Mean annual incisor wear =			2,29	1,55	1,03

Table 7.2. cont..../- 133 -

Table 7.2. cont.

4. Age group 10 to 11 years

No. of animal	No. of days between marking and recapture	Age when marked (years)	Annual wear (mm)		
			I_1	I_2	I_3
W 7	400	10	2,65	2,19	1,07
R F	380	10	1,87	1,15	1,46
R U	341	10	1,37	1,42	-
R 7	384	11	2,57	1,33	1,34
R T	373	11	3,38	2,87	-
R 11	365	10	2,75	2,10	1,73
	Mean annual incisor wear =		2,43	1,84	1,40

5. Age Group 12 to 14 years.

R 12	531	12	2,23	2,05	1,48
B 4	406	14	2,45	2,20	1,48
B 2	370	14	2,76	2,42	1,33
	Mean annual incisor wear =		2,48	2,22	1,43

By determining the mean infundibular lengths for I_1 and I_2 (Table 7.1.) it was possible to calculate at what ages these infundibula would be completely worn away. This was done by adding the expected wear of successive years together until the total represented the mean length of the corresponding infundibulum. The theoretical values thus obtained indicated that all enamel from the infundibula of I_1 and I_2 would be worn away on their table surfaces at 15 and 16 years respectively. When cutting the bits of animals of various ages down to 15 or 16 years, it was found that the eventual wearing away of infundibula can be used as very accurate ageing criteria. By this

method of..../- 134 -

method of reproducing field wear, a series of age classes could be defined without having to follow individual animals throughout their life. In all cases the artificial stages obtained by cutting the incisors were similar to those of animals where natural wear had taken place, i.e. the pattern on the table surface of each incisor was the same.

The method of cutting an incisor was as follows:-

(i) the labial surface of each incisor was coated with a thin layer of black paint. Using vernier callipers, set for the amount of incisor wear to be cut off, a line was drawn across the black paint onto the enamel. This line was intensified by scratching the enamel across the labial surface of the tooth with a very fine-tipped tungsten lathe blade. This was done for the six incisors of each specimen,

(ii) using the clear scratch on the enamel as a guide, the respective sections were cut off each tooth by running the saw blade parallel to the table surface,

(iii) an electric grindstone was then used to grind the tooth down exactly to the level of the scratch in the enamel.

(iv) cut incisors were then replaced into their alveoli so that the picture provided by the table surfaces could be assessed,

By arranging each differently aged bit into a series, from younger to older ages, it was possible to define the age classes ((1) to (27)).

7.2. Results..../- 135 -

7.2. Results

7.2.1. Age Classes defined.

Using the available data in the described way the following 27 age classes were recognised. The age classes from birth to animals $3\frac{1}{2}$ years old have each been divided into an"A" and a "B" section. Section "A" represents fresh skulls i.e. live animals or skulls before any meat or other tissue around the teeth has been removed. Section "B" represents old skulls i.e. skulls cleared of all soft tissue adhering to the teeth or bone. The "Prints" referred to under the various age classes are copies made of actual carbon prints from selected animals and these have been used to illustrate some of the age classes (3 to 27) instead of making use of photography (Fig. 7.23).

1) New born foals.

A. Id_1 just erupted or possibly not yet erupted through the gum. Occasionally late term foeti have Id_1 erupted. No sign of Id_2 or Id_3 (Fig. 7.13.).

Parts of Pd_2 and Pd_3 just piercing the gum (i.e. the longest cusps). Pd_4 not yet erupted but can be felt through the gum. (Fig. 7.14.).

B. Whole table surface of Id_1 visible through premaxilla; Id_2 and Id_3 only partially visible, i.e. have not yet erupted beyond the level of their alveoli (Fig. 7.15.).

Pd_1 visible but not yet erupted beyond the level of its alveolus. Pd_2 to Pd_4 erupted. M_1 not yet erupted but visible in its alveolus. (Fig. 7.15.).

2) One to..../- 136 -

Fig. 7.13. New born foal. Note that the form of Id_1 can been seen below the gum.

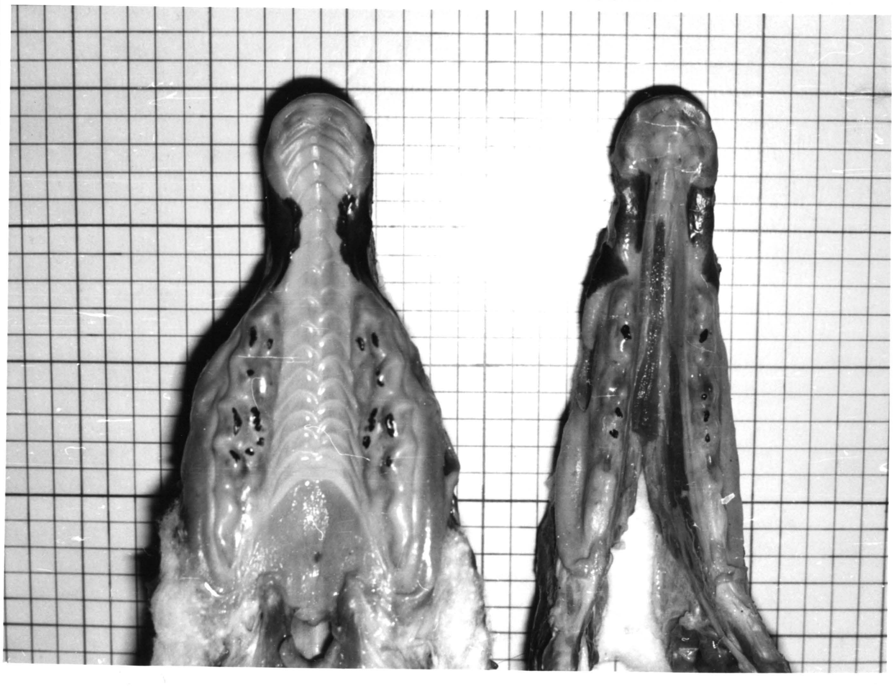


Fig. 7.14. New born foal. Left=upper and right=lower jaw. Pd_2 and Pd_3 are just starting to pierce the gum. The position of the advanced cusps are given by the black dots.

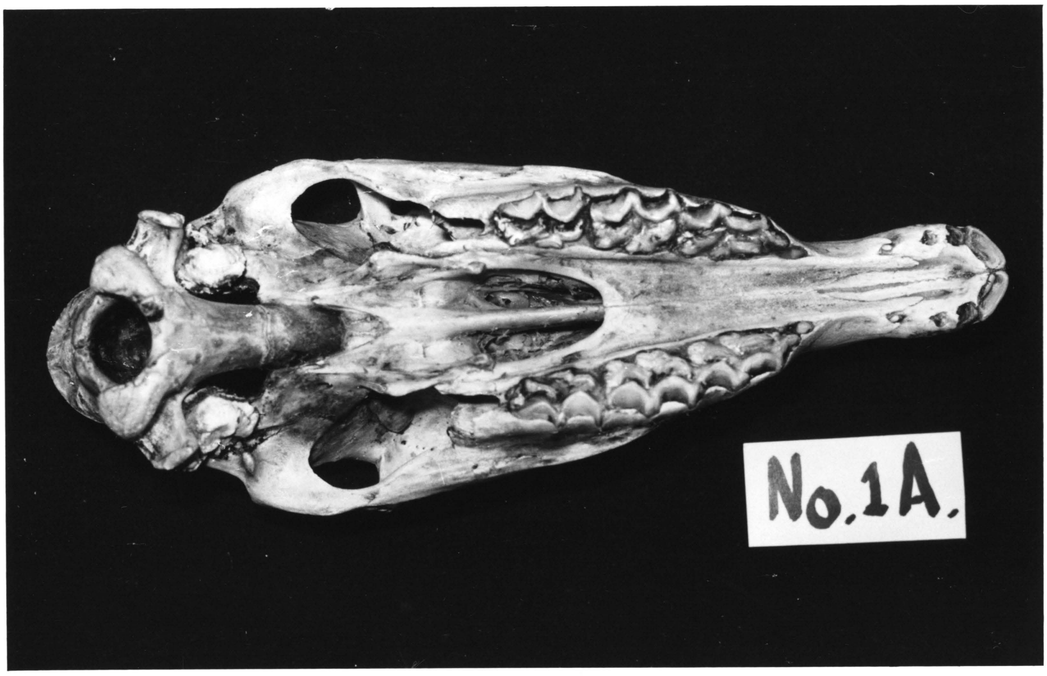


Fig. 7.15. Skull of new born foal.

2) One to 7 days.

A. No incisors may be visible, but Id_1 usually erupts during this stage; Id_2 can be felt through the gum.

Longest cusps of Pd_4 just piercing the gum; Pd_2 and Pd_3 only partially erupted (Fig 7.16.).

B. Id_1 and Id_2 completely visible through the premaxilla (i.e. the whole table surface); Id_3 has not yet erupted beyond the level of its alveolus and only the tip is visible (Fig. 7.17.).

3) One to 2 weeks.

A. Id_1 just starting to wear; Id_2 can be felt through the gums. Towards the end of this age class Id_2 may just have erupted. (Fig. 7.18. and Fig. 7.23, Print 3).

Pd_2 to Pd_4 almost completely erupted through gum and showing first signs of wear; Pd_1 not yet erupted through gum.

B. Id_3 approaching the surface of the premaxilla; both lingual and labial edges and infundibulum of Id_3 visible.

Pd_2 to Pd_4 in wear.

4) Two weeks to 3 months.

A. Id_2 erupted and starting to wear; Id_2 about 3 mm above gum level; no sign of Id_3 (Fig. 7.2 3, Print 4).

Pd_2 to Pd_4 completely erupted through gum and totally in wear; Pd_1 usually erupted through the gum and may be in wear.

B. Id_3 projecting beyond the level of its alveolus, but not yet completely erupted.

M_1 clearly visible in its alveolus.

5) Three to..../- 137 -

Fig. 7.16 One to 7 days old.

Fig. 7.17. One to 7 days old.

Fig. 7.18. One to 2 weeks old.

5) Three to 6 months.

A. Id_3 can be felt through the gum or has partly erupted (Fig. 7.23, Print 5). (Id_3 usually erupts at about five months).

No sign of M_1.

B. Whole table surface of Id_3 erupted beyond the level of its alveolus (Fig. 7.19).

M_1 approaching the maxillary bone, but not yet projecting beyond it; M_2 frequently visible in its alveolus. (Fig. 7.19.).

6) Six to 9 months.

A. Whole table surface of Id_3 erupted, but not yet in wear; Id_1 and Id_2 fully in wear (Fig. 7.23, Print 6).

M_1 can be felt through the gum.

B. Table surface of Id_3 more or less parallel with those of Id_1 and Id_2.

M_1 projecting beyond surface of maxilla; M_2 visible in its alveolus.

7) Nine months to 1 year.

A. Id_3 just starting to wear (Fig. 7.23, Print 7).

Longest cusps of M_1 erupting through gum, but not yet in wear.

B. Grinding surface of M_1 completely erupted through maxilla; M_2 clearly visible in its alveolus and approaching the surface of the maxilla (Fig. 7.20.).

8) One to $1\frac{1}{2}$ years.

A. Id_3 about half in wear (Fig. 7.23, Print 8).

M_1 starting to wear; M_2 can be felt through the gum.

B. M_2 erupted through maxilla; M_3 may be visible in its alveolus.

9) $1\frac{1}{2}$ to 2..../- 138 -

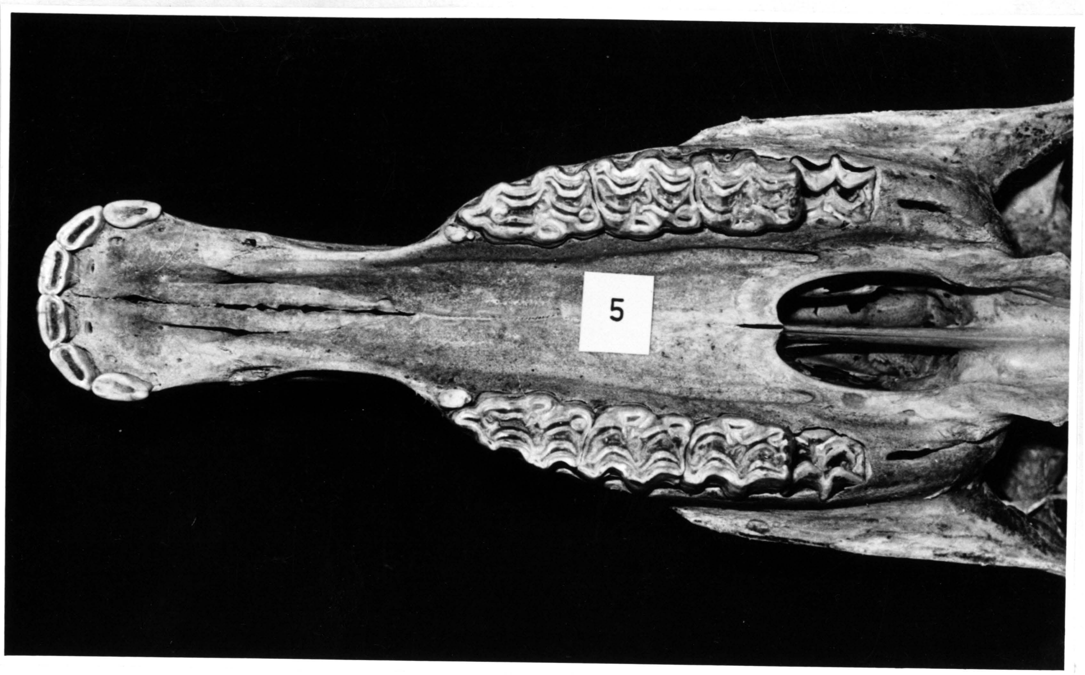


Fig. 7.19. Three to 6 months old.

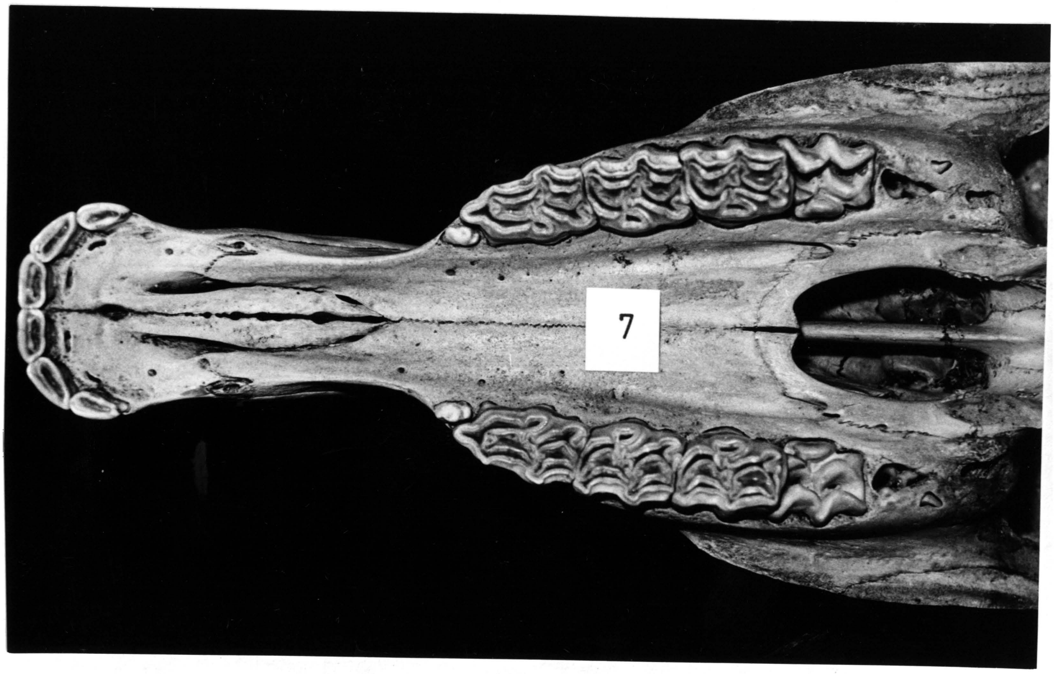


Fig. 7.20. Nine months to 1 year old.

9) $1\frac{1}{2}$ to 2 years.

A. Id$_3$ three-quarters in wear (Fig. 7.23, Print 9).

M$_2$ erupting and just starting to wear.

B. Id$_1$ a short stump that may be easily dislodged; I$_1$ visible below Id$_1$ (Fig. 7.21.).

M$_3$ visible in its alveolus (Fig. 7.21.).

10) Two to $2\frac{1}{2}$ years.

A. I$_1$ replaces Id$_1$; Infundibulum of Id$_2$ almost worn away; Id$_3$ usually fully in wear (Fig. 7.23, Print 10).

M$_2$ fully in wear.

B. M$_3$ approaching maxilla but not yet projecting through it (Fig. 7.22); Upper edge of P$_2$ and sometimes P$_3$ visible below the stumps of Pd$_2$ and Pd$_3$ respectively.

11) $2\frac{1}{2}$ to 3 years.

A. I$_1$ in wear; Id$_2$ and Id$_3$ short stumps (Fig. 7.3a and Fig. 7.23, Print 11).

M$_3$ can be felt through the gum or has started to erupt; Pd$_2$ and Pd$_3$ replaced by P$_2$ and P$_3$ respectively; Pd$_4$ a short stump.

B. C visible in its alveolus (♂♂).

M$_3$ projecting above surface of maxilla; Upper edge of P$_4$ visible below stump of Pd$_4$.

12) $3\frac{1}{4}$ years.

A. I$_2$ replaces Id$_2$ but is not yet in wear; table surface of Id$_3$ flat and almost without an infundibulum (Fig. 7.23, Print 12).

M$_3$ erupted but not yet fully in wear.

B. In..../- 139 -

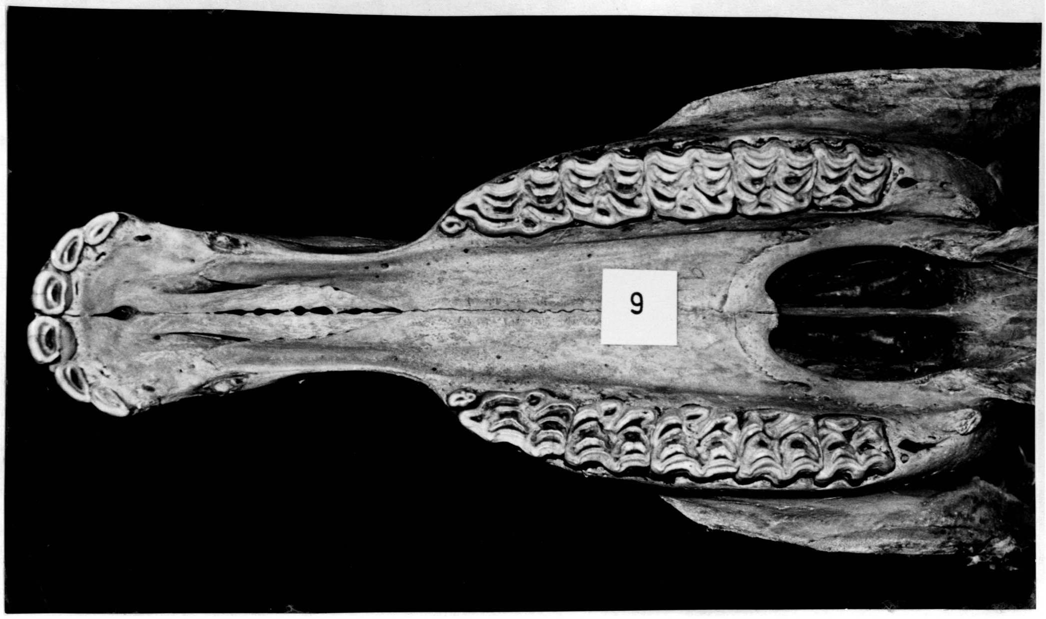


Fig. 7.21. 1½ to 2 years old.

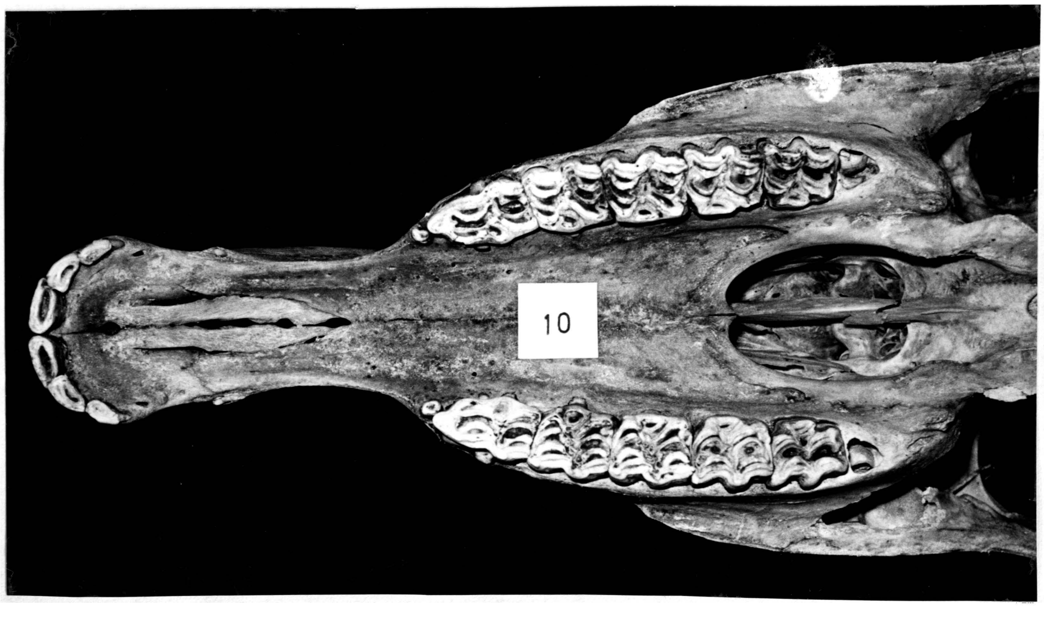


Fig. 7.22. Two to 2½ years old.

B. In stallions C has erupted past the surface of the premaxilla. Stumps of Pd_4 loose and easily removed (Fig. 7.1.).

13) $3\frac{1}{2}$ years.

A. I_2 in wear; Id_3 a short stump; C erupting in stallions. (Fig. 7.23, Print 13).

Pd_4 replaced by P_4; M_3 fully in wear. P_4 may or may not be in wear.

B. I_3 can be seen in its alveolus just posterior to Id_3.

14) Four years.

I_3 replaces Id_3 but is not yet in wear (Fig. 7.23, Print 14). All premolars and molars in wear.

15) $4\frac{1}{2}$ years.

I_3 wearing on labial side; Infundibula of I_1 to I_3 long (Fig. 7.23, Print 15).

16. Five years.

Lingual side of I_3 just in wear; Infundibula of I_1, I_2 and I_3 long-oval (Fig. 7.23, Print 16).

17) Six to 7 years.

Infundibula of I_1, I_2 and I_3 long-oval (Fig. 7.23, Print 17).

18) Eight to 9 years.

Infundibulum of I_1 oval; of I_2 and I_3 long-oval (Fig. 7.23, Print 18).

19) Ten years.

Infundibulum of I_1 oval; of I_2 oval to long-oval; of I_3 long-oval (Fig. 7.23, Print 19).

20) Eleven years.

Infundibulum of I_1 round-oval; of I_2 oval; of I_3 long-oval. (Fig. 7.23, Print 20).

21) Twelve..../- 140 -

21) Twelve years.

Infundibulum of I_1 round; of I_2 round-oval; of I_3 oval. (Fig. 7.23, Print 21).

22) Thirteen years.

Infundibulum of I_1 round and small; of I_2 round; of I_3 oval. (Fig. 7.23, Print 22).

23) Fourteen years.

Infundibulum of I_1 a tiny spot; of I_2 round; of I_3 round-oval. (Fig. 7.23, Print 23).

24) Fifteen years.

Infundibulum of I_1 absent but mark still present; of I_2 round and small; of I_3 round; table surface of I_1 equilateral triangle. (Fig. 7.23, Print 24).

25) Sixteen years.

Infundibulum of I_2 absent but mark still present; of I_3 round and small; table surface of I_1 isoceles triangle, longer than wide; of I_2 equilateral triangle. (Fig. 7.23, Print 25).

26) Seventeen years.

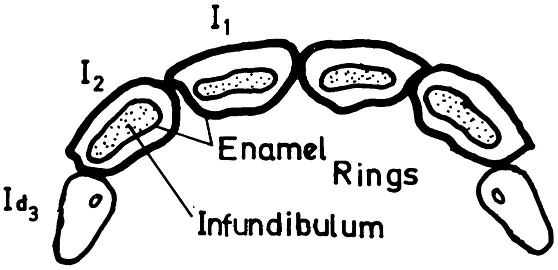
Infundibulum of I_3 absent but mark still present; table surface of I_1 long isoceles triangle; of I_2 equilateral triangle; of I_3 more or less equilateral triangle (Fig. 7.23, Print 26).

27) Eighteen to 20 years.

Table surface of I_1 rectangular; of I_2 isoceles triangle to rectangle; of I_3 irregular rectangle (Fig. 7.5, c & d and Fig. 7.23, Print 27.).

7.3. Discussion..../- 141 -

Fig.7.23.

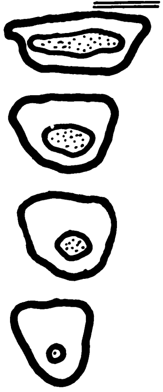


I_1, I_2 & I_3 = Incisors one two & three. (Permanent)

Id_1, Id_2 & Id_3 = Deciduous Incisors one two & three

W = WEARING

Shape of Infundibulum



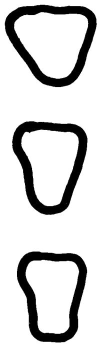
= Long-oval

= Oval

= Round-oval

= Round

Shape of Table Surface

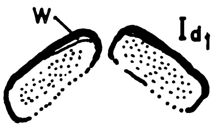


= Equilateral Triangle

= Isosceles Triangle

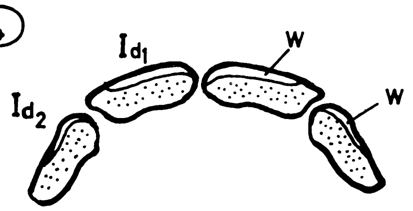
= Rectangular

③



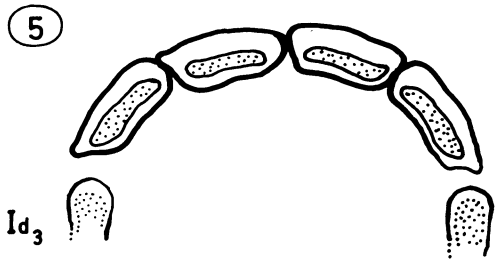
1-2 weeks

④



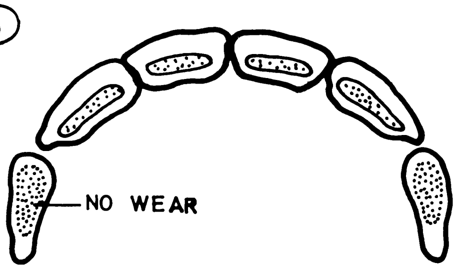
2 weeks - 3 months

⑤



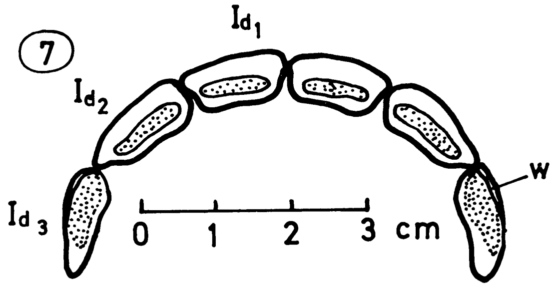
3-6 months

⑥



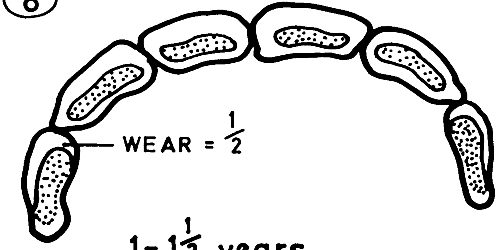
6-9 months

⑦



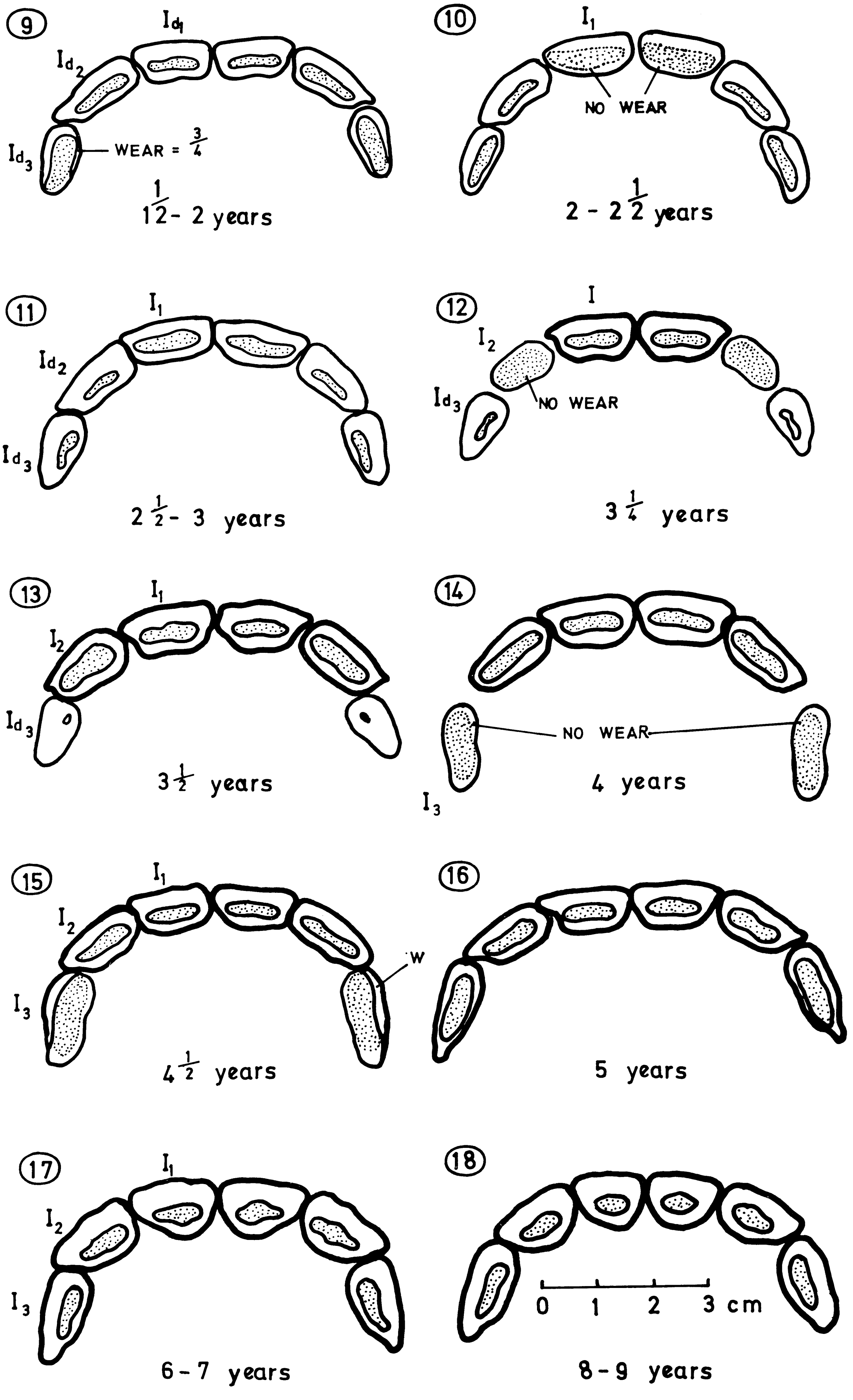
9months - 1 year

⑧



1 - 1$\frac{1}{2}$ years

Fig. 7.23.



⑨ $1\frac{1}{2}$- 2 years

⑩ 2 - $2\frac{1}{2}$ years

⑪ $2\frac{1}{2}$- 3 years

⑫ $3\frac{1}{4}$ years

⑬ $3\frac{1}{2}$ years

⑭ 4 years

⑮ $4\frac{1}{2}$ years

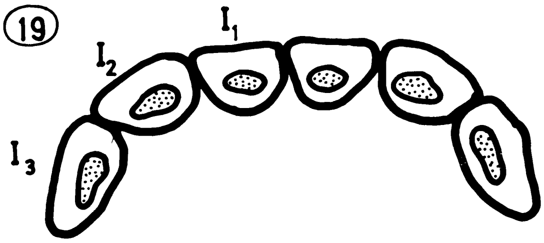
⑯ 5 years

⑰ 6 - 7 years

⑱ 8 - 9 years

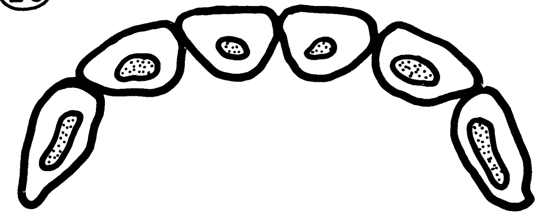
Fig.7. 23.

⑲



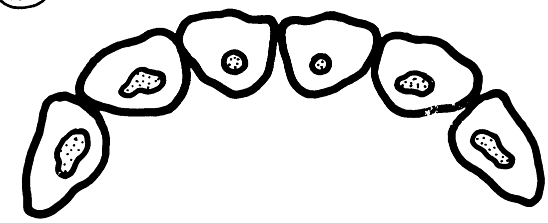
10 years

⑳



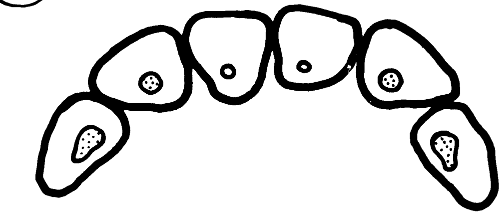
11 years

㉑



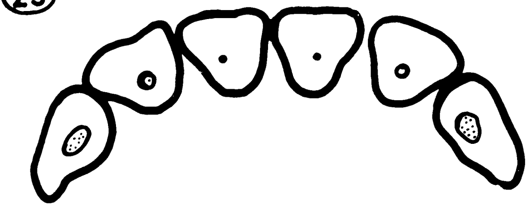
12 years

㉒



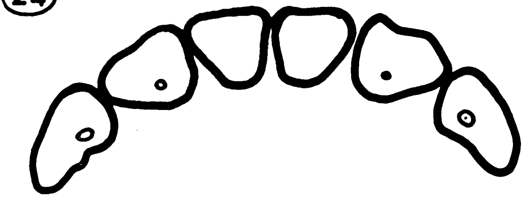
13 years

㉓



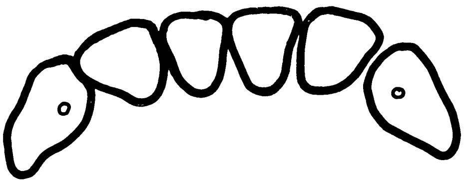
14 years

㉔



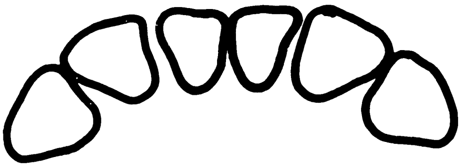
15 years

㉕



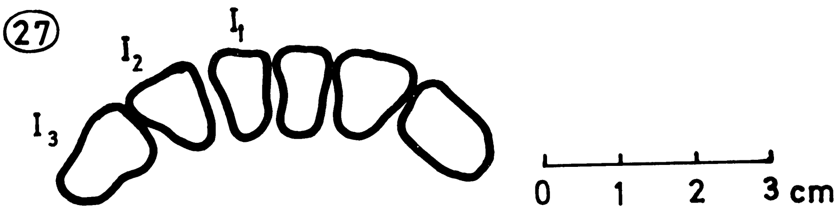
16 years

㉖



17 years

㉗



18 - 20 years

7.3. Discussion.

For age classes 1 to 15 (i.e. up to 4½ years) it is possible to age zebra very accurately as stages of wear can be used together with the eruption and replacement of incisiform and molariform teeth. Observations on both captive and free roaming zebra have shown that up to this age the accuracy indicated by the age classes is justified, as there is very little variation between individuals. The numerous overlapping criteria used also tend to obviate any inaccuracies. Possibly the most important point is that many of the age classes are exactly the same as those defined by Klingel and Klingel (1966), while others differ only in that they cover longer or shorter periods of time, the actual criteria being the same. The value of accurate age classes up to 4½ or five years of age is extremely important in the zebra, since it is within this period that major changes (physiological and psychological) affecting the reproduction and population dynamics of the species take place.

In age classes 16 to 27 (five to 20 years of age) inaccuracies are more likely to occur since there is individual variation between animals, while unevenly worn incisors are fairly common (Fig. 7.5.). In general the accuracy of the system decreases in the very old age classes (15 to 20 years). Although many of the age classes span a period of one year, this degree of accuracy is not implied, as a 16 year old animal with evenly (normally) worn incisors could quite conceivably be 15 or 17 years old. The accuracy of the technique is, however, aptly substantiated by the minimal overlap obtained between it and the method of counting the cementum layers (Table 7.3.).

When comparing the older age classes (16 to 27) of my system

with the..../- 142 -

with the corresponding series described by Klingel and Klingel (1966), one finds that there is a difference of one to three years between the same criteria. In Klingel's system, for example, the infundibulum of I_1 is worn away at between 11 and 13 years (say 12 years), while in my system this occurs at 15 years (difference = ± 3 years). The same disparity is found when comparing the wear of I_2 and I_3. Additionally, when one moves up to the younger age classes in both systems, the disparity between corresponding criteria decreases from three to about one year and eventually in animals younger than $4\frac{1}{2}$ years, there is no difference. The discrepancy between the two systems is possibly due to:

(i) The mean infundibular length for the first incisor (I_1) in East African zebra is 27,0 mm (Klingel and Klingel 1966) while for Kruger Park zebra the mean length is 31,03 mm. This would account for a difference of almost $1\frac{1}{2}$ years in the ageing. Unfortunately Klingel does not give figures for I_2, otherwise this could have served as an additional check.

(ii) The remaining inequality could be due to a difference in the rate of incisor wear between the two regions - the Kruger Park zebra having slower incisor wear than the East African sub-species.

Table 7.3..../- 143 -

Table 7.3.

Examples of the difference between ageing zebra by the cementum method and the infundibular method.

Age (years) (Infundibular method)(1)	Age (years) (Cementum method) (2)	Difference between 1 and 2 (i.e. 1 minus 2) (years)
3½	3½	0
4½	5	- ½
5	4½	+ ½
5½	7	-1½
6	6	0
6	5½	+ ½
7	8	- 1
7	6	+ 1
8	9½	-1½
8	7½	+ ½
8	8	0
9	10	- 1
10	9	+ 1
11	11½	- ½
11	10½	+ ½
11	9½	+1½
13	14	- 1
17	16½	+ ½
19	21	- 2
19	18½	+ ½

As far as the tooth cementum technique is concerned, one has at one's disposal a quick and accurate method of checking and in some cases developing ageing criteria. The method is, however, unpractical for routine use on large samples, but could be used on selected specimens, especially when old age and uneven bits make ageing difficult.

In contrast..../- 144 -

In contrast to zebra, the technique is being generally used to age impala and according to Graupner (pers. comm.) is also a very practical method for ageing the blue wildebeest (Connochaetes taurinus). In South Africa, where mammals are subjected to very definite winter and summer seasons, cementum annuli appear to be clearer than in the same species found in the tropics, where green vegetation may be available throughout the year. Although the counting of tooth cementum layers sounds extremely simple, it is in fact a laborious task to produce a suitable section. Also the cementum rings are not equally clear in all specimens (Fig. 7.10. and 7.11.) and a number of sections may have to be cut before a favourable count can be made.

Due to the availability of other more practical and accurate ageing techniques, the eye lens technique must be regarded as being valueless for ageing zebra. This is largely due to (i) the immense size of the lens (wet weights often exceed 3 gms) and hence the amount of time required to dry it, and (ii) the reduced rate of weight increase after four years of age which results in a large overlap of lens weights between age classes (Fig. 7.0.). Because of this overlap the technique is of little value for evaluating the age classes derived by measuring incisor wear. The linear correlation between age and eye lens weight after four years of age does, however, indicate that the ageing criteria are valid. (Laws, 1967). With regard to the shape of the curve one finds that as with the pronghorn antelope (Kolenosky and Miller, 1962), the impala, (Fairall, 1969) and the African elephant (Laws, 1967), there are two growth phases. Initially there is a period of rapid lens growth (up to about 4 years of age), followed by a phase showing a rectilinear relationship with age. It is interesting to note that

between 3½..../- 145 -

between $3\frac{1}{2}$ and four years of age zebra stallions reach sexual maturity and testis weights reach their adult maximum. In the work of Laws (1967) where he was able to separate his sample into males and females, one finds a similar break in the curve for the female African elephant at about eight years. This is also the approximate age at which cows become sexually mature (Buss and Smith, 1966; Perry, 1953). In the case of the bulls the break occurs at about nine years, this also being the approximate age of puberty (Johnson and Buss, 1967). A similar relationship seems to exist in the impala and the kudu - see Fairall (1969) and Simpson and Elder (1968), and is probably true for for many mammal species.

Although zebra frequently live to over 20 years of age in zoological gardens (record = 28 years one month 24 days) (Fowler, 1931), a maximum ecological longevity of 22 years seems very feasible. Supporting this is the fact that in a sample of over 700 culled zebra only one animal was in the age class 18 to 20 years, while in a sample of 200 skulls collected from predator kills, there were five (All 200 skulls being those of adult animals). In addition to this, one skull from a group of old one's selected for ageing by the cementum method, was found to be 21 years old. By the time zebra reach this age the incisors are worn down to short stumps which are frequently level with the gum. Cutting a naturally worn 17 year old bit down to 20 years produces an I_1 of total length 2 - 2,5 cms. This tooth cannot be pushed out much further, since the feeding process would tend to dislodge it. One thus comes to the conclusion that the longevity of free-roaming wild zebras, as with the African elephant, is largely determined by the condition of their teeth. The fact that zebra gen-

erally live..../- 146 -

erally live longer in zoological gardens is not only due to the absence of predation, but also to a less fibrous and abrasive diet and the consequent reduced wear of incisors, premolars and molars. In the wild state old zebra find it increasingly difficult to maintian themselves due to the condition of their teeth and soon succumb to predators. It would be interesting to know to what age a zebra would live (in the Kruger Park) in the absence of predation.

SUMMARY..../- 147 -

SUMMARY

Since the initiation of the first management policies in the Kruger National Park in 1902 the zebra (Equus burchelli antiquorum H. Smith, 1841) population has shown a marked increase in numbers. Although this increase has largely been confined to certain regions of the Park, it has been amplified by the concomitant increase in numbers of other large herbivores, while species such as the roan antelope, sable antelope and tsessebe have declined in numbers. In addition to fluctuations in the numbers of herbivores, vegetational changes have taken place. In many instances these changes have been unacceptable to the species here considered.

With the initiation of essential management practices such as disease control, water provision, burning programs and the fencing of the western boundary of the Park, the culling of excess zebra in certain areas has also become necessary. To calculate more reliable culling quotas and to decide on the most effective distribution of artificial watering points, it has been deemed necessary to gain a knowledge of the factors affecting the zebra's choice of habitat, distribution, home range size, and to trace their seasonal and migratory movements.

Since this project is actually the forerunner of a detailed study on the reproduction and population dynamics of zebra, and since animals were regularly captured for marking purposes, a simultaneous study could also be made on a method of ageing the species.

All zebra were marked with coloured "sterkolite" collars, no two animals bearing similar collars. Data on 52 zebra marked between

1963 and..../- 148 -

1963 and 1965 were augmented by over 1200 resightings collected between 1969 and 1971 on an additional 89 marked animals. This data has helped to divide the zebra population of the Kruger National Park into eight ecologically self-sufficient sub-populations. These sub-populations, although not separated from each other by impassible barriers, were found to retain their identity with a minimum of mixing occurring between units.

By analysing the seasonal timing of movements, the direction, the distance and the regularity, it was further possible to decide whether a particular sub-population is sedentary, semi-migratory or migratory.

The only truly migratory zebra are found in the central district where they undertake a regular, north-south migration between winter (dry season) and summer (wet season) ranges. The extent of the migration was found to be up to 75 kilometres, while the time taken to complete the movement could vary between two and 17 days, depending on conditions. The stimuli involved in zebra migration and the question as to whether migratory behaviour is instinctive or traditional are also discussed.

Semi-migratory zebra, with the exception of the zebra of the Pretoriuskop-Malelane-Skukuza area, were found to undertake west to east movements, the extent and duration of which depend on rainfall. To a large extent these zebra move from the Lebombo flats into the Lebombo hills during the wet season. Zebra in the Pretoriuskop-Malelane-Skukuza area, on the other hand, were found to undertake a very different type of movement which was largely dependent on the rotational burning programs carried out in the area.

Sedentary..../- 149 -

Sedentary sub-populations such as the zebra in the Satara area undertake wet season movements which take them away from the permanent waterholes to previously underutilized areas. These areas are not situated in any particular direction or distance from the winter range. Here the summer grazing areas form a mosaic pattern around the winter areas.

Of the factors affecting the zebra's choice of habitat, distribution, movements and migration, water and grazing conditions were found to be the most important. In addition to these, factors such as topography, soil type, thicket density, inter- and intra-specific competition, predator pressure and sociality also affect movements. Zebra were found to avoid areas which were waterlogged and where the sticky soil conditions impeded normal locomotion.

Using the resighting data on marked animals it was possible to calculate the yearly home range size for 50 groups. These home ranges sizes were found to vary considerably from sub-population to sub-population, the largest mean size (207 sq. km) being for the Pretoriuskop-Skukuza-Malelane sub-population and the smallest (111 sq. km) being for the Crocodile Bridge sub-population. Variations in home range size could not be correlated with inter- or intra-specific intolerance, but rather with characteristics of the particular habitat and its general acceptability to zebra.

Using the skulls of over 700 culled zebra together with data collected both in the field and on captive zebra kept at Skukuza, it was possible to define 27 age classes for zebra between birth and 20 years of age. These age classes are based on the eruption and wear of deciduous and permanent incisors, premolars and molars. The age

classes of..../- 150 -

classes of adult animals were obtained by direct measurement of the annual wear of each individual incisor. Since these animals are aged according to the shape of the table surface of each incisor and the shape of the corresponding infundibulum, the incisor teeth could be cut down by the amount that they would have worn in two or three years, and the shape could again be assessed. In addition to this, carbon prints were made of the table surface of each marked animal's incisors and these animals were recaptured after six and 12 or 18 months. By comparing prints made at these intervals it was possible to asses the changes occurring in naturally wearing incisors and to correlate this with teeth cut down by the same amount of "measured" annual wear.

The accuracy of the abovemetnioned technique has aptly been substantiated by the discovery of annual growth rings in the cementum of the permanent incisors. By counting growth rings it has also been possible to decide on a maximum ecological longevity for the zebra of some 22 years.

OPSOMMING..../- 151 -

OPSOMMING

Sedert die instelling van natuurbeheer in die Krugerwildtuin in 1902, was daar 'n besliste toename in die getalle van die kwagga (Equus burchelli antiquorum, H. Smith, 1841). Alhoewel hierdie toename in getalle hoofsaaklik beperk is tot sekere dele van die Wildtuin, word dit bevestig deur die daarmee gepaardgaande groei in getalle van ander groot plantvreters, terwyl species soos die bastergemsbok, swartwitpens en tsessebe weer in getalsterkte gedaal het. Behalwe die fluktuering in die getalle van plantvreters, het daar ook veranderings in die plantegroei plaasgevind. In baie gevalle was laasgenoemde veranderings onaanneemlik vir die species onder bespreking.

Met die instelling van essensiële beheerpraktyke soos die kontrole van siektes, watervoorsiening, gekontroleerde veldbrand en die oprigting van 'n heining op die westelike grens van die Wildtuin, het uitdunning van oortollige kwaggas in sekere areas ook noodsaaklik geword. Om meer betroubare uitdun-kwotas toe te ken en om die mees doeltreffende verspreiding van kunsmatige waterbronne vas te stel, is dit nodig geag om inligting te bekom oor die faktore wat die kwagga se habitatsvoorkeur, sy verspreiding en die grootte van sy tuisgebied bepaal, asook om seisoenale- en trekbewegings na te spoor.

Aangesien hierdie projek eintlik die voorloper is van 'n meer omvangryke studie oor die reproduksie en populasiedinamika van die kwagga, en daar gereeld kwaggas gevang en gemerk moes word, kon terselfde tyd 'n studie van ouderdomsbepaling tegnieke gemaak word.

Elke kwagga is gemerk met 'n gekleurde 'sterkolite' nekband. Data is versamel van 52 kwaggas wat tussen 1963 en 1965 gemerk is,

sowel as..../- 152 -

sowel as van 'n verdere 89 gemerkte diere wat tussen 1969 en 1971 meer as 1200 keer waargeneem is. Hierdie data het dit moontlik gemaak om die kwagga-populasie van die Krugerwildtuin in agt ekologies-selfonderhoudende sub-populasies in te deel. Daar is gevind dat hierdie sub-populasies, alhoewel hulle nie deur onoorkomelike versperrings van mekaar geskei is nie, tog hul identiteit behou het met 'n minimum van vermenging tussen die eenhede.

Deur die seisoenale tydsberekening van bewegings, die rigting, die afstand en die reëlmatigheid te ontleed, was dit verder moontlik om te bepaal of 'n spesifieke sub-populasie sedentêr, semimigrerend of migrerend is.

Die enigste werklik migrerende kwaggas word in die sentrale distrik gevind waar hulle gereelde, noord-suid migrasies onderneem tussen winter (droë seisoen) en somer (nat seisoen) weidings gebiede. Die afstand waaroor die trekke plaasgevind het, was tot so ver as 75 km, terwyl die voltooiing daarvan, afhangende van omstandighede, van twee tot 17 dae kon duur. Die stimuli wat by hierdie migrasies betrokke is, asook die vraag of trekgedrag instinktief of tradisioneel is, word ook bespreek.

Daar is gevind dat semi-migrerende kwaggas, met die uitsondering van die in die Pretoriuskop-Malelane-Skukuza area, van wes na oos trek en dat die distansie en duur daarvan van reënval afhanklik is. Tot 'n groot mate beweeg hierdie kwaggas vanaf die Lebombo-vlaktes na did Lebombo-heuwels gedurende die nat seisoen. Kwaggas van die Pretoriuskop-Malelane-Skukuza area daarenteen, volg heeltemal 'n ander bewegingspatroon wat sterk beinvloed word deur die rotasie brandprogram in die area.

Sedentêre..../- 153 -

Sedentêre sub-populasies soos die kwaggas in die Satara area, beweeg in die nat seisoen weer weg van standhoudende watergate af na voorheen onbenutte areas. Hierdie areas is nie in enige spesifieke rigting of afstand van die winterweiding af nie. Hier vorm die somerweidingsareas 'n mosaiekpatroon rondom die winter-areas.

Van die faktore wat kwaggas se habitatsvoorkeur, verspreiding, bewegings en migrasie beïnvloed, is water en weidingstoestande die belangrikste. Behalwe bogemelde, word bewegings ook beinvloed deur faktore soos topografie, grondtipe, digtheid van die boom- en struikstratum, inter- en intraspecifiese kompetisie, roofdierdruk en gemeenskapsin. Daar is gevind dat kwaggas areas wat deurnat is en waar normale voortbeweging gestrem word deur klewerige modder, vermy.

Deur die data te gebruik wat verkry is uit die herhaalde waarneming van gemerkte diere was dit moontlik om die jaarlikse tuisgebiedgrootte vir 50 groepe te bereken. Daar is gevind dat die grootte van die tuisgebied aanmerklik variëer van een sub-populasie na 'n ander en dat die grootste gemiddelde grootte (207 vk. km) dié van die Pretoriuskop-Malelane-Skukuza sub-populasie en die kleinste (111 vk. km) dié van die Krokodilbrug sub-populasie was. Variasies in tuisveldgroottes kon nie gekorreleer word met inter- en intra-specifiese onverdraagsaamheid nie, maar eerder met eienskappe van die besondere habitat en die algemene aanvaarbaarheid daarvan vir die kwaggas.

Deur die skedels van meer as 700 uitgedunde kwaggas te gebruik, tesame met data wat verkry is van sowel kwaggas in die veld as van kwaggas wat op Skukuza aangehou is, was dit moontlik om 27 ouderdomsklasse vir diere tussen geboorte en 'n ouderdom van 20 jaar te onderskei. Hierdie ouderdomsklasse is gebaseer op die erupsie en

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slytasie van tydelike sowel as permanente snytande, voorkiestande en kiestande. Die ouderdomsklasse van volwasse diere is verkry deur die direkte meting van die jaarlikse slytasie van elke individuele snytand. Aangesien hierdie diere se ouderdom vasgestel word volgens die fatsoen van die bytoppervlakte van elke snytand en die fatsoen van die ooreenstemmende infundibulum, was dit moontlik om van elke snytand dieselfde hoeveelheid te verwyder as wat in twee of drie jaar sou afslyt en die fatsoen dan weer vas te stel. Hierbenewens is koolafdrukke gemaak van die bytoppervlakte van die snytande van elke gemerkte dier en die diere is weer gevang na ses en 12 of 18 maande. Deur die koolafdrukke wat met hierdie tussenposes gemaak is te vergelyk, was dit moontlik om die veranderings wat natuurlike slytasie in tande teweeggebring het, vas te stel en te korreleeer met tande waarvan dieselfde hoeveelheid 'gemete' jaarlikse slytasie verwyder is.

Die akkuraatheid van bogemelde tegniek is paslik gestaaf deur die ontdekking van jaarlikse groeiringe in die cementum van die permanente snytande. Deur die groeiringe te tel, was dit ook moontlik om vas te stel dat die maksimum ekologiese lewensduur van die kwagga sowat 22 jaar is.

ACKNOWLEDGEMENTS..../- 155 -

ACKNOWLEDGEMENTS

The author hereby wishes to acknowledge the support recieved from the following persons or instances:

The Director of National Parks, Mr. R. Knobel and The National Parks Board of Trustees who not only granted the necessary permission and financial aid, but who allowed the author to continue with the project after his permanent appointment.

My promotor, Professor F.C. Eloff of the University of Pretoria, for his help and encouragement during the study.

My co-promotor Dr. U de V. Pienaar, Assistant Director of Nature Conservation in the Kruger National Park, for his stimulating interest in every aspect of the project. Dr. Pienaar introduced the author, then a novice, to the project, and was always available to offer advice and encouragement.

The Council for Scientific and Industrial Research (CSIR) (Pretoria) for a post-graduate research grant of R500.00 received during 1969.

The Rembrandt Tobacco Corporation of South Africa for a bursary of R300.00 received during 1969.

The late Deputy Director of National Parks, Mr. R.J. Labuschagne, with whom the author communicated in connection with a post-graduate research grant from the National Parks Board of Trustees.

Dr. N. Fairall, former Assistant Biologist in the Kruger National Park, for his help and ideas while planning the project.

Mr. P. van Wyk, Chief Research Officer in the Kruger National Park, who offered enthusiastic advice and wbo was always ready to help with the identification of plant specimens.

Mr. G.L. van ..../- 156 -

Mr. G.L. van Rooyen, Instrument Maker in the Kruger National Park, whose help and advice with the use of capture and marking equipment was most valuable. Also for permission to use his machinery and tools both when making the collars and when cutting and grinding the zebra teeth.

The Deputy Director of National Parks, Mr. A.M. Brynard, who, in his former capacity as Nature Conservator in the Kruger National Park, contributed toward the success of the project.

Dr. G. de Graaff, Assistant Director, Nature Conservation, Cape Parks, who was most helpful and enthusiastic about getting the maps and diagrams printed.

Mr. H. Braack and his wife Tony, Technicians in the Kruger Park, who were always keen to help with any aspect of the project.

District Rangers J.H. de Kock and M.C. Mostert and Senior Ranger S.G. Botha, for their stimulating interest and help, either in the field or with the collection of resightings from marked animals. District Ranger J.J. Kloppers, for his advice on the movements of zebra in the northern district. Chief Ranger F.D. Lowe, District Ranger G.M. Adendorff, Senior Rangers A.J. Espag, D.C. Ackerman and D.C.Swart and Rangers D.S. Roux, E.A. Whitfield and T.B. Mollentze, for the resightings which they faithfully reported.

Mr. J. Shepherd, former Game Catcher, and Mr. C.J. Lombard, former Senior Technician, who helped with the initial capture and marking of zebra.

Mrs. A.M.M.C. Prinsloo, Librarian, and Mrs. P.Y. Wood, Assistant Librarian, who were of great assistance in the location and collection of suitable references. Mrs. Prinsloo was also kind enough to translate the summary.

All the..../- 157 -

All the staff of the Engineering and Tourism sections in the Kruger National Park, who unselfishly collected and forwarded the resighting forms to the author. In this respect a special word of thanks to Mrs. M. van Achterbergh.

Mr. J. Marais and his staff at the culling depot, who provided labour and help when marked zebra were being destroyed for ageing purposes.

Mr. S. Schoeman and his associates at the drawing office, who offered valuable advice and help on the compilation of suitable maps.

Mrs. M. van Niekerk, who undertook the typing of this thesis and for the conscientious way in which the work was done.

Mr. A.O. Zaayman, Official Photographer of the National Parks Board, who took the series of photographs on the collection of data from the teeth of marked zebra and who undertook the developing and printing of numerous of the photographs used in this treatise.

Mr. K.G.L. Mills, who did a fine job of correcting the grammatical and punctuation mistakes in the text.

All the Natives who assisted at various times in this study, in particular Jutai Lubisi and Philemon Chauke, who frequently had to work overtime and under trying conditions.

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